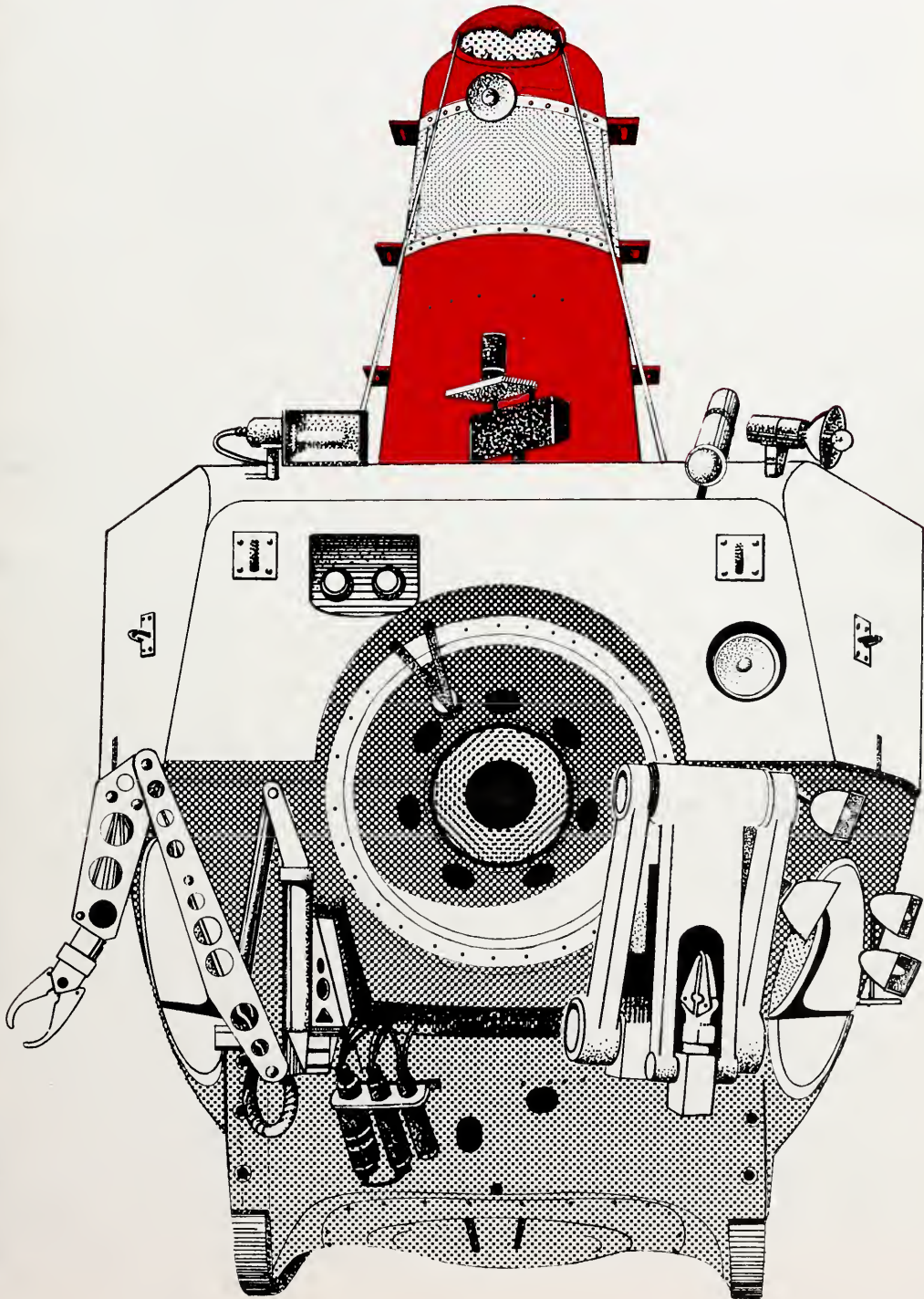


# Oceanus

Volume 23, Number 2, Summer 1980



# Oceanus<sup>®</sup>

The International Magazine of Marine Science

Volume 23, Number 2, Summer 1980

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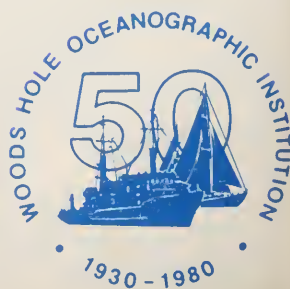
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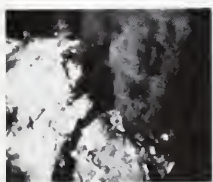
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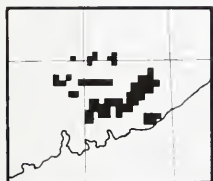
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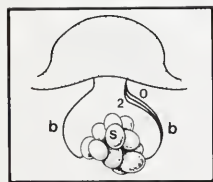
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FRONT COVER: Artist E. Kevin King's rendering of the submersible Alvin, operated by the Woods Hole Oceanographic Institution. The submarine's latest exploits are described on page 18. BACK COVER: "Black smoker" on the East Pacific Rise (see page 24). Photo by Robert Ballard.

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# Patterns in Plankton

by John H. Steele

Human beings are not distributed uniformly over the surface of the earth. Our density has patterns on many different scales. Populations are generally sparse in deserts and dense where the soil is productive; or they tend to concentrate along coastlines. And, on very small scales, we build houses in relation to particular terrains or water supplies. Yet, outside these external constraints and between the largest and smallest scales, we ourselves determine much of the pattern of human activity. In the past, the size of market towns and the distance between them would depend on the limited mobility of two or four feet. Now, the changing distributions within and between cities are functions of the railroad, the car, and the airplane. Thus, like all other organisms, we are partly dependent, partly independent of our physical and chemical environment; and the consequences can be seen in the way populations aggregate in towns, in herds, or on shoals.

The oceans may appear to be much more uniform than the land. Marine organisms might be expected to be spread more evenly through the water than their terrestrial counterparts. Yet the pelagic terrain can be as rugged as the earth's surface. The temperature and salinity change with increasing depth and also can change abruptly at "fronts" that divide one part of the ocean from another in the same way that a mountain range can divide a forest from a desert. So we find that broad regions of the ocean, such as the Sargasso Sea or the Antarctic, can have very different levels of basic productivity. And, at the other extreme, we have to consider the behavior of individuals or small groups on scales of meters or millimeters. Between these limits, in the oceans as on land, we see patterns of distribution on all scales and we ask the same questions. Are these patterns determined by the

physical environment, or do the organisms, in a sense, create their own environment within their food web, and is this seen in the way they are distributed?

There are certain regularities in size and composition of open-ocean food chains that we do not find on land. The plants living in the upper layers of the ocean are microscopic, with diameters usually in the range of 5 to 50 microns. The herbivores that feed on these are crustaceans ranging from the size of rice grains to small shrimp. In turn, the animals that prey on these herbivores can be small fish—or whales. Thus there is a regular progression in size as we climb the trophic ladder (unlike trees, which are grazed on by caterpillars). Also, there is an increase in longevity from a few days for the marine plants to several years or decades for some of the predators. The increase in length of life from days to months to years roughly balances the decrease of approximately 90 percent in productivity as we go one level up in the trophic system. The result is that the standing stocks at each trophic level may be about the same order of magnitude (Sheldon and others, 1972). But this level of biomass can be very different for large areas of the ocean (Figure 1). It is these estimates of the productivity of general ocean regions combined with knowledge of the trophic level at which we harvest that have provided information on the maximum probable yield that we can take from the sea by present conventional methods. The total predicted yield of around 100 million tons (Ryther, 1969; Bell, 1978) comes almost entirely from coastal and upwelling areas. This is true partly because these areas are more productive than the open ocean, but, more important, because in the former regions we harvest at trophic levels much closer to the primary plant production.

These general limitations on our yield from the sea have been described in *Oceanus*, Vol. 22, No. 1, 1979. Also, there and elsewhere, consideration has been given to the consequence

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*Unloading catch at Provincetown, Massachusetts. Man's predation patterns have changed with the advent of new technology. (Photo by Hank Simmons, PR)*



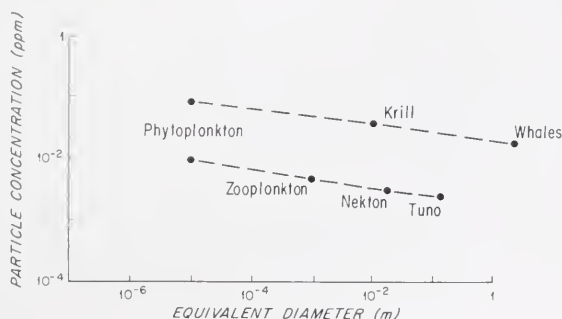


Figure 1. Estimates of standing stock in terms of particle concentration for different trophic groups in two regions; upper line, Antarctic; lower line, equatorial Pacific (Sheldon and others, 1972).

of harvesting at lower trophic levels than our present methods permit. If we accept the large-scale average picture implicit in Figure 1, then there is the same or slightly greater concentration of biomass at the lower levels, but these also will be about ten times more productive. On this basis, if fishing were merely a question of harvesting the average organic matter in the water, then removing smaller organisms should be as efficient as capturing large ones, but since the overall productivity is so very much higher, the total yield could be correspondingly greater. It is this potential that has tested the ingenuity of technologists. The flaw in this picture is that we do not have an environment with average concentrations. If we did, predation would not be ecologically or economically feasible. This is true not only for fishermen but also for the natural predators in the sea. Thus we need to consider the nature of the variability and the limitations on aggregation for different groups of organisms.

I have described the very large-scale limitations on productivity imposed by the environment. The physical and chemical conditions present other small-scale limitations on the concentrations of the primary producers — the phytoplankton. Since the microscopic plants depend on the nutrients in the water as well as on light for their growth, the concentration of these nutrients in the upper layer will generally determine the maximum amount of plant material in, say, a cubic meter of the sea. In coastal regions, the maximum winter concentration of nitrate (10 to 20 milligram atoms per cubic meter) will give a crop of about 10 grams biomass\* per cubic meter, equivalent to a concentration of  $10^{-5}$ . Figure 2 demonstrates both the dependence on nutrients and the small-scale patchiness that can occur during the early stages of a phytoplankton bloom.

These plants have a relatively short life span as individual cells, perhaps 1 to 5 days, and have very little capability of movement through the water. By sinking, they can increase their concentration, particularly when the water itself is rising, and this can, very occasionally, produce larger densities, such as those found in red tides (see *Oceanus*, Vol. 21, No. 3, p. 41).

In subtropical regions of the open ocean, such as the Sargasso Sea, nutrient concentrations are rarely greater than a tenth of coastal maxima and usually very much less. Correspondingly, this imposes a very much smaller upper limit on plant concentration. In this way, the range of concentrations for the base of the food chain is closely defined by the physics and chemistry of the environment. The small herbivorous crustacea that graze on this plant material have a longer lifetime, on the order of 30 days, and are capable of vertical motion, usually migrating from deeper water to feed at night in the surface layers. Since the upper and deeper layers can have different horizontal motions, the vertical migration can provide a means for lateral movement and, in turn, permit aggregations of these small animals in larger patches. Patches on scales of about 30 to 50 kilometers are observed in the North Sea (Cushing and Tungate, 1963; Steele, 1974) and can be contoured by sampling with plankton nets (Figure 3). If we assume that, at night, they are in the upper few meters, then their concentration can reach levels of about 100 grams biomass per cubic meter (Mackas and Boyd, 1979).

Pelagic fish or mammals, such as herring or whales, feed on these herbivores. These organisms are capable of directed movement — migrations

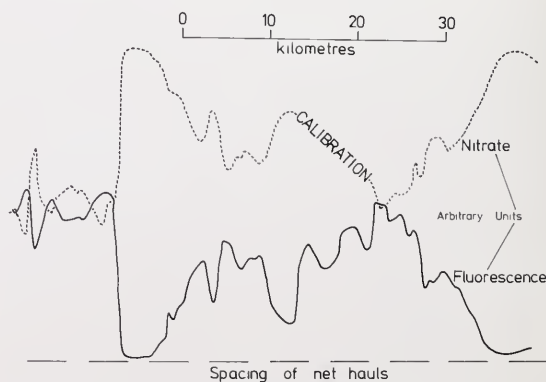


Figure 2. Small-scale patchiness of nutrients and phytoplankton indicated by the fluorescence of the pigments. These data were collected in early spring in the surface waters of the North Sea. The inverse relation shows the dependence of plant growth on a major nutrient, nitrate. The lines along the bottom indicate the coarser sampling obtainable with conventional plankton nets, which will not reveal smaller-scale structure.

\* Assuming a biomass/nitrogen ratio of 70:1.



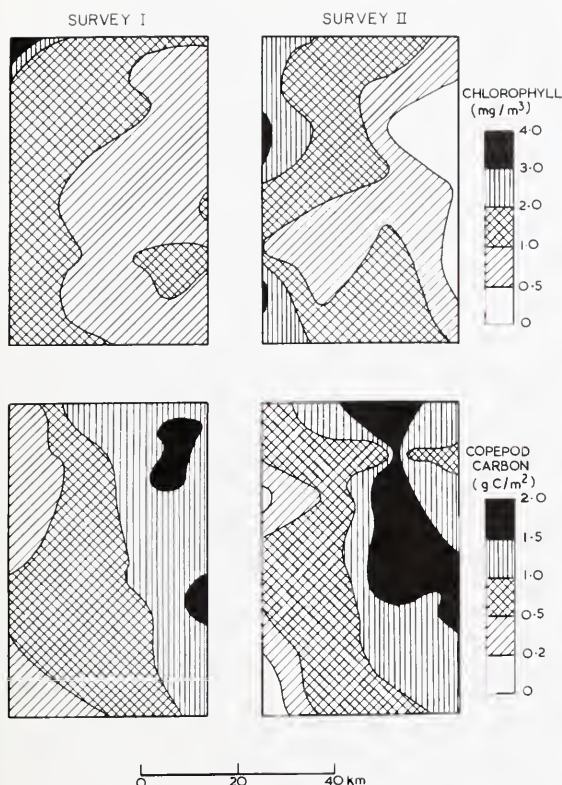


Figure 3. Larger-scale patchiness of phytoplankton (chlorophyll) and herbivorous zooplankton (copepods) in summer in the North Sea when the plant distribution is more influenced by grazing and the general inverse relations of plants and animals can be seen at scales between 1 and 100 kilometers (Steele, 1974; Mackas and Boyd, 1979). Surveys I and II were separated by a 3-day interval.

that permit them to travel long distances to aggregate on their food wherever it is at high concentration. These patterns of migration are not completely known, nor well understood. Many of the pathways are along ocean fronts where there are sharp changes in the physical character of the environment. Thus the pelagic organisms use these signs to guide their movement around the ocean to regions where food is abundant or to areas where they aggregate for mating and spawning. In this way, they make use of features in their surroundings rather than being controlled by them as are those organisms in the lower trophic levels (Figure 4).

Thus during their lifetime these predators can be found over very wide areas of the ocean but at any instant may be located in a small region. Within this locality, they will occur in densely packed schools or shoals so that a cubic meter of water can contain several kilograms of fish.

For these reasons, we obtain a very different picture when we consider maximum concentrations rather than average levels. Perhaps the best illustration of this difference is found in the Antarctic when we compare the mean values of Figure 1 with the maximum values on a cubic meter basis in Figure 5. There is a relatively small increase for the phytoplankton dependent, as described, on the ability to convert nutrients into organic matter. The herbivores, krill, are known to swarm in relatively dense aggregations (Omori, 1978). For the baleen whales, which are predators on the krill, if we choose the appropriate cubic meter, then the concentration of organic matter in that cubic meter is unity!

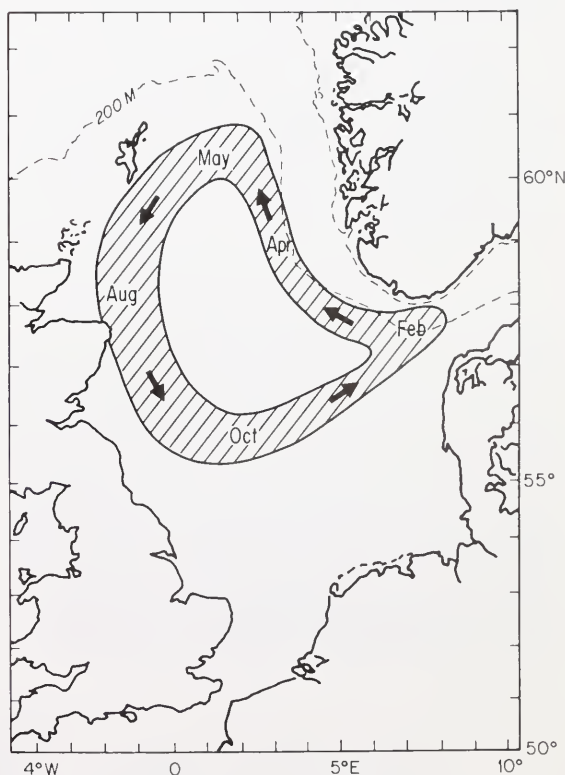


Figure 4. The migration path of herring around the northern North Sea, according to Cushing (1955). The northerly movement in the spring is along the western edge of less saline water from the Baltic that flows up the Norwegian coast. The south and eastward fall migration is along the general axis of Atlantic inflow (Dooley, 1974). Thus much of the migratory circuit corresponds to current systems, as well as to food concentrations (Steele, 1961).

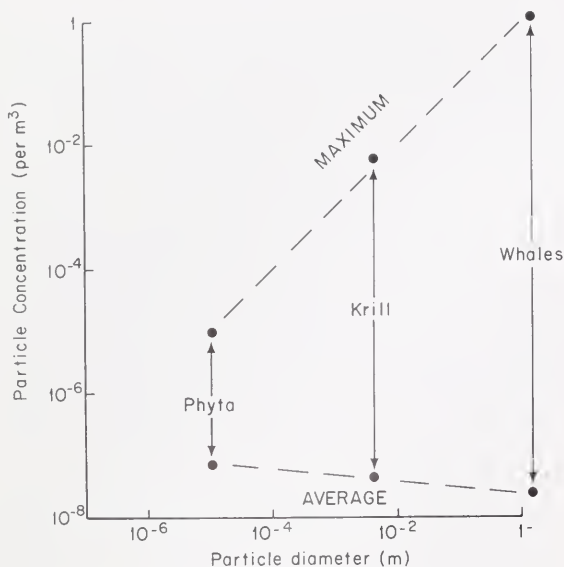


Figure 5. A comparison of average concentrations in the Antarctic with the maximum based on possible concentrations of organic matter in a cubic meter.

The choice of a cubic meter, which represents a ton of water or biomass, is appropriate for the next predator, man, since this is the unit in which he measures the "bites" that he takes from the ocean whether this be herring, whales, or, potentially, krill.

These features of increasing patchiness with the steps up the trophic ladder illustrate how the various populations have adapted to life in the basically dilute medium of the open sea. It is unlikely that any group could survive if it had to feed on the average, so each has evolved to concentrate where food is most plentiful, in turn supplying adequate sustenance for the level above. Thus, as we go from plants to herbivores to predators, we see less response to the structure of their physical surroundings and a corresponding ability to use the larger-scale features of the ocean system such as fronts or currents. In turn, this ability makes them less directly dependent on local or short-term events such as storms which will have marked effects on phytoplankton production and



Krill is the food of whale and man alike: above, the Antarctic species *Euphausia superba* (5 centimeters).

concentration. So the biological "behavior" — social or individual — of the higher trophic levels plays a more dominant role.

On the other hand, if successful feeding can take place only on above-average concentrations of the food, then this can supply an ecological refuge for the food organisms by removing predation pressure on the below-average concentrations. Thus the increasing patchiness with increasing steps up the trophic ladder can provide both for efficient energy transfer and for population survival (Figure 6).

Baleen whales, for example, feed on the dense swarms of krill. Thus the growth rate of the whales and, especially, the excess of food energy for reproduction depends on the number and density of these swarms and the whales' ability to locate them. It is interesting that as the whale population has declined the time taken to reach maturity also has decreased, while their fecundity has increased (Laws, 1977). This would indicate some inverse relation between whale population density and availability of the dense concentrations of their food. Such a relation can help to produce a natural balance between prey and predator populations.

If, however, the pelagic predators, such as herring, are assumed to be gathered in a localized area and, within that area, concentrated in shoals, then the low density refuge may not exist for predation upon them. In this case, it appears that the relatively large size of the shoals provides for the population a defense against predators, such as dolphins which are individually much smaller than the prey unit if we take that unit to be a shoal. This convoy theory appears to be a possible explanation of how a population balance could be achieved with natural predators operating near the top of the food chain.

How does this work when we come to another top predator — man? There are two reasons why we harvest at or near the top of the natural food chain. The organisms are relatively large and therefore economically more desirable. Because of their large size, they are easier to remove from the water, especially when we do this by straining the organisms from the water with a net. But, as I have tried to show, the main reason is the existence of increasingly dense aggregation of that organic matter (Figure 6).

How does man himself fit into this pattern proposed for other predators? How has he adapted to his role as a top carnivore? Initially, his behavior was similar to that of land-based predators, such as seals, with a defined range and thus a localized impact, spatially and seasonally. Also, the methods of fishing, with drifting nets capturing individual fish from a dense shoal, might not be too different from those of the other natural predators, both

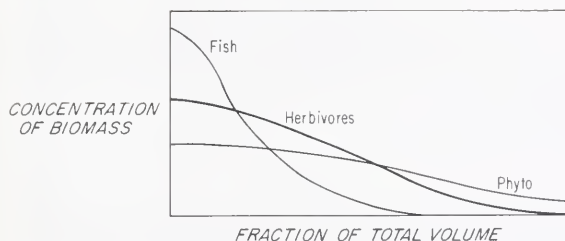
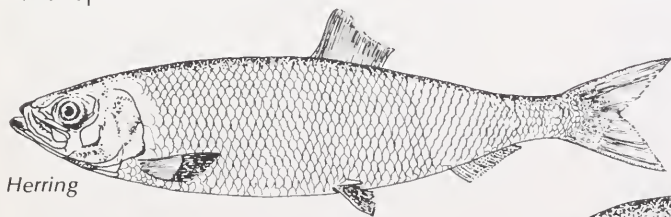


Figure 6. Schematic, and hypothetical, instantaneous distributions depicting the relation between concentration of three trophic levels and the fraction of the upper layers of the ocean that they occupy. Thus, at any instant, most of the pelagic fishing will occur in a relatively small fraction of the total volume, whereas the phytoplankton are more evenly spread.

capturing a significant fraction without attacking the "tail" of the distribution (Figure 6).

The development of technology has changed the nature of this predator not merely quantitatively but also qualitatively. The fishing vessels have a much greater range and capacity, but the main feature is their ability to regard a whole school or shoal as the unit of prey, searching for these units with sonar and engulfing them with a purse seine. Thus there has been not only an increase in efficiency but also a change in the nature of this predator. This evolution, resulting from technology, has been relatively rapid with no noticeable adaptation by the individual prey species. The consequences of the change in predation pattern have been extreme for these target species, such as herring or anchovy. Yet in most cases the whole ecosystem appears to have adapted by restructuring or rebalancing the food web so that the energy made available is absorbed in other pathways. In the North Sea, for example, there seems to have been a replacement of herring and mackerel, partly by smaller and less economically desirable pelagic fish and partly by an increase in groundfish such as haddock and whiting which do not have such marked seasonal concentrations in particular areas. In the Antarctic, calculations of the present day energy flows within the food web do not indicate a pronounced surplus of krill. Rather, it appears likely that other predators have replaced the whales.



Herring



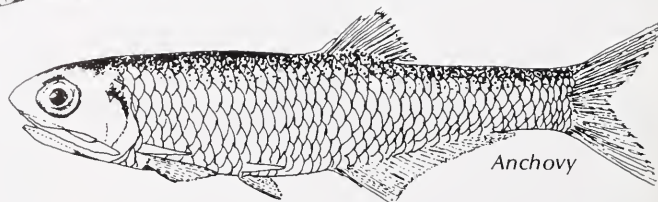
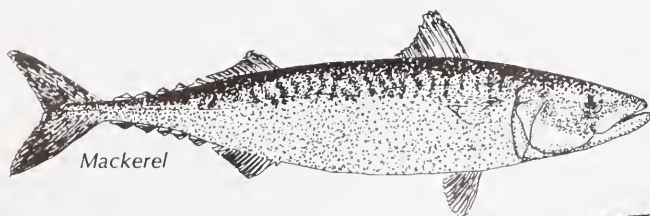
Haddock

The economic consequences to fisheries of these changes have been severe, but what is relevant here is the ecological and behavioral patterns. The virtual collapse of these pelagic fisheries is the result not so much of the number of predators — the fishing boats — as of the ability of these predators to take their prey as easily at low as at high densities. This newly created imbalance results not from changes in the average populations of prey and predator over large areas but from interactions on relatively small scales where a change in "bite" size can switch the system from a stable to an unstable relation. This switch depends on the behavior of the prey. The fact that for herring the catch per unit effort does not decrease significantly as population levels fall, suggests that with decreasing stocks, the fish still form the same size shoals and are thus as easily captured.

Analogies are necessarily incomplete and may delude rather than illuminate. Yet there is a certain attractive formalism in the comparison of successively higher trophic levels in the sea with advancing human structures. There is an increasing independence of the detailed components of the physical and chemical environment. A greater degree of social aggregation provides the basis for a more efficient utilization of resources. Yet the economies of scale can create their own problems. For the seas, at least, it is apparent that our understanding and our management of these ecosystems depend on a knowledge not only of the larger-scale averages but also of the smaller-scale variability.

For these reasons, much of the interest and attention in our research is focused on these intermediate scales where the interactions of plants and animals are partly but not wholly determined by the physical conditions. My illustrations have been taken from the distribution of phytoplankton because we have methods to measure continuously the concentration of their photosynthetic pigments in the upper layers. But we know that part of the variations we observe must be the result of grazing on the plants by the herbivorous crustaceans. It has proved more difficult to obtain comparable data on this component of the food web, in part because their vertical movements preclude using measurements at one depth as an index. We have





certain natural experiments, such as the study of zooplankton populations trapped in Gulf Stream rings, which are eddies detached from the Stream and moving through the alien environment of the Sargasso Sea (Wiebe, 1976). These eddies with scales of about 100 kilometers and lifetimes of 100 days have the correct dimensions for study of zooplankton populations. The changes in these populations provide an index of the response to the changed environment.

Our interest in these herbivorous components of the food web is not only because of their important role within that web but also because we can think of harvesting them as a source of human or animal foodstuff. There have been some minor attempts at harvesting in the Northern Hemisphere, in Norwegian and Japanese waters, and mainly as bait for sport or commercial fishermen. But the best known possibility is the Antarctic krill where the available resource could be comparable to our present total world yield of fish. The potential for initial harvesting involves numerous economic and technical factors but depends ultimately on the ability to locate and capture the dense swarms. How do the swarms aggregate in relation to physical features? Can one define the behavioral components of the concentrating mechanisms? Continued exploitation will be related to the response of the population to intensive fishing. Will the swarms decrease in size and concentration? Or will they be replenished from peripheral and less dense communities? Will the controlling mechanisms that appear to operate with whales also apply to large, predatory, krill boats? These questions display the links between the basic ecology and the problems of management; and the dependence of both on our understanding of the interactions between large-scale productivity and small-scale pattern. The former controls the overall possible yield, the latter determines how we as well as the natural predators can take this yield economically and safely.

John H. Steele is Director of the Woods Hole Oceanographic Institution.

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# EL NIÑO:



## Lessons for Coastal Fisheries in Africa?

by Michael H. Glantz

There is a mystique surrounding scientific research that attempts to forecast future states of the environment, probably stemming from the belief that more information can only be beneficial. The mystique is often generated by no more than wishful thinking about the value of such research; but in some instances that value has not been determined. A good example is the attempt to develop an environmental forecast of the meteorological-oceanographic phenomenon known as El Niño, which has an adverse effect on the biological productivity in Peruvian coastal waters, ultimately affecting Peru's anchoveta fishery (see *Oceanus*, Vol. 21, No. 4, p. 40). It is widely believed that such a reliable forecast would supply the scientific information needed to manage the fishery rationally. One might argue, on the other

hand, that considerable scientific information about the fishery already exists, and that what is needed is a better use of these data rather than large quantities of new information.

In addition, the call for more scientific research often tends to shift attention toward geophysical processes and away from social, political, and economic questions. However, it may be within the social processes that solutions to many questions about environmentally rational fisheries management lie. Assessing the societal value of such a forecast as an exercise in identifying the role of scientific information in the development of a healthy fisheries sector is of interest not only to Peru but also to other developing countries that border coastal upwelling regions, such as Mauritania and Somalia, which are in the process of expanding their commercial fisheries operations.

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*Above, part of Peru's anchoveta fleet in harbor.*

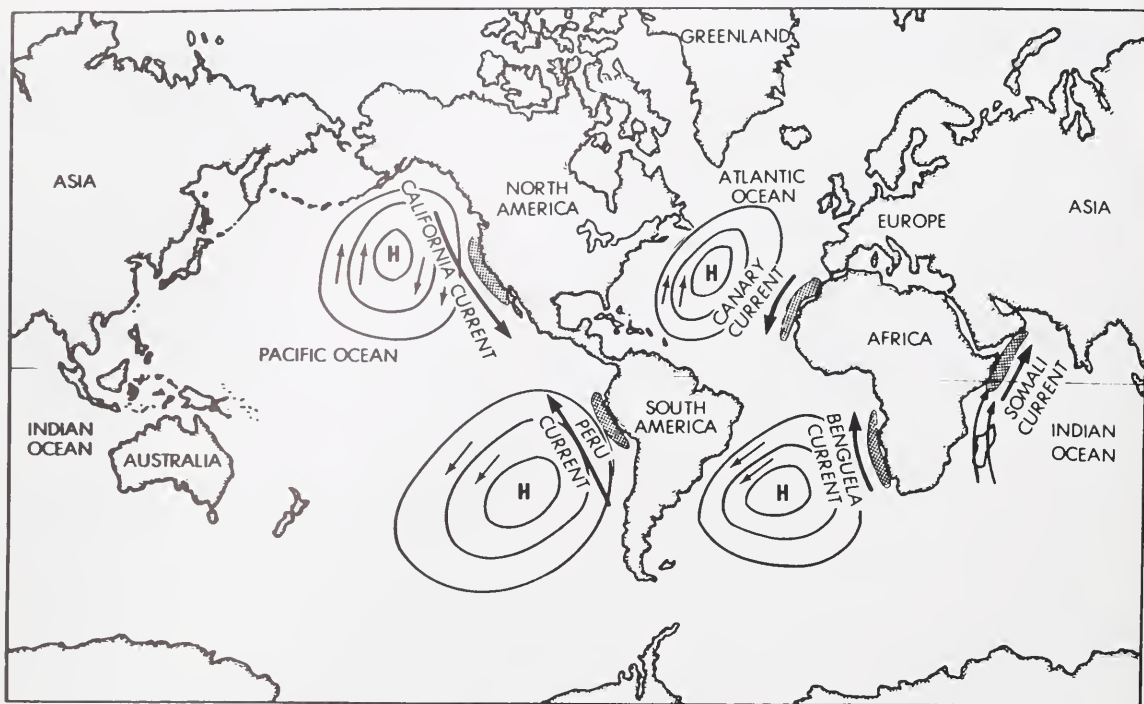


Figure 1. Major coastal upwelling regions of the world and the sea-level atmospheric pressure systems (anti-cyclones) that influence them.

### Peru and El Niño

In terms of biological productivity, the Peruvian coastal zone is one of the five major coastal upwelling areas in the world (Figure 1). El Niño (in Spanish, referring to the Christ child because it usually occurs at Christmastime) is the name given to a sporadic invasion of warm, nutrient-poor surface water into the eastern equatorial Pacific that tends to overshadow the naturally occurring coastal upwelling processes in which deep, nutrient-rich cold water is brought upward into the sunlit or euphotic zone. The sudden depletion of nutrients in the upper sunlit layers of the ocean adversely affects phytoplankton and zooplankton production, thereby disrupting the food chain. The result (of which El Niño is probably only a link in a series of events\*) is that fish populations are also adversely affected. Fish apparently become widely dispersed in their search for food, recruitment is reduced, and a high density of anchoveta appears

near the coast where some pockets of cold, nutrient-rich deep water upwell to the surface.

Before 1970, Peru's fishing industry underwent a rapid expansion, with catches sometimes doubling annually (Figure 2). By the mid-1960s Peru, registering about 22 percent of the world's commercial catch by tonnage, was considered to be one of the world's leading fishing nations. At that time, physical and economic conditions appeared favorable for continued expansion of the anchoveta fishery.

But optimism waned in 1972-73 when a major El Niño event occurred. At its onset, the effect was hardly noticed. Large numbers of anchoveta were found close to shore, in high-density pockets where upwelling to the surface still occurred despite the general invasion of warm, nutrient-poor surface water into the area. Record catches were taken in so short a time that the size and age distribution of the fish could not be assessed, variables that might have given insight into the condition of the standing stock. Later assessments showed that excessive fishing had already cut heavily into the standing stock of anchoveta during 1971, when the year-class recruitment had been a poor one. Thus, at the very time when (according to many observers) there should have been less fishing, the opposite occurred.

\*Teleconnections is a word used by meteorologists to describe apparent correlations between meteorologically related phenomena in different parts of the world—in this instance between El Niño, cold winters in the United States and Europe, weakening of the Indian monsoon, heavy rains and unusual hurricane activity in the Pacific, and droughts in the Sahel and in northeast Brazil.



After the sharp reduction in biological productivity and anchoveta landings in 1972-73, the Peruvian government nationalized the fishing industry, ostensibly to preserve the anchoveta resource, but also to fulfill economic objectives. In 1976-77, a policy of denationalization was pursued because the anchoveta had not returned in large numbers and the government could no longer subsidize fishermen or workers in fish processing plants.

It generally has been assumed that with a reliable El Niño forecast, the depletion of anchoveta stocks could have been avoided, which in turn would have mitigated, if not averted, the economic, political, and social dislocations that resulted from the reduced productivity of the fishery. Hence, the argument goes, an El Niño forecast ought to be of great value to decisionmakers in Peru and elsewhere.\* There has been a great interest within the scientific community to develop such a capability.

### El Niño Forecast Value

Experts knowledgeable about El Niño, Peru, and the fishmeal industry — in government, fisheries management, the physical sciences, economics, and public policy within and outside Peru — were asked in an open-ended mail survey by the author in 1977 what they thought might be the value of an El Niño forecast two to four months in advance of the event. They were asked to suggest what might have been done in 1972 had there been a reliable forecast. Responses included such opposing views as tying up the fishing fleet until a year or so after the El Niño had passed, thus protecting the standing stock of anchoveta; and allowing all-out fishing, either to thin the stock so the remainder could have a better chance of survival, or because many of those caught would die anyway. Both views were based on the belief that the government wanted to manage the fishery so as to preserve the resource for exploitation in future generations; but the lack of consensus in the scientific community about the connection between an El Niño and biological productivity led the respondents to their opposing views.

Other suggestions included closing the fishery and subsidizing various sectors of the fishing industry, increasing fishmeal storage capacity and holding stocks in reserve to be sold at elevated prices during future El Niño events, sharply reducing the fleet and number of fishmeal plants, appointing a sole authority to manage the fishery, and shifting from the northern to the southern zone on the Peruvian-Chilean border.

\*The anchovy is reduced to a higher-value export product, fishmeal, which in the early 1970s was exported to markets in the United States and Western Europe as a feed supplement for poultry, swine, and cattle.

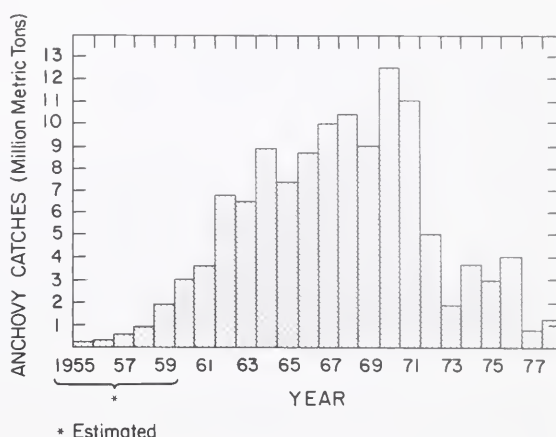


Figure 2. Before 1970, Peru's fishing industry underwent a rapid (some say meteoric) expansion with catches in its early years doubling annually.

Survey respondents also identified some of the constraints that might diminish the value of an El Niño forecast, such as the relatively short lead time (two to six months); forecast unreliability; the constantly changing characteristics of El Niño — intensity, duration, and magnitude; and, perhaps most important, political and economic constraints. Scientific information is only one aspect that will figure into decisions made by a fisheries policymaker; it will be integrated with economic and political considerations, which often tend to outweigh the rational scientific arguments for cautious exploitation of the anchoveta fishery.

Even if there were specific data on the relationship between an El Niño forecast and biological productivity, such information would not necessarily be properly used. There have been reports on the Peruvian fisheries issued before 1972 that could be considered forecasts; however, the implicit or explicit warnings in those reports were not incorporated into the decisionmaking processes in any significant way. For example, one report written by R. C. Murphy in 1954 for the Peruvian Guano Administration noted that unless management was oriented toward conservation of the anchoveta fishery, not only would the fishery collapse, but the guano industry as well.\*

In 1969 the Peruvian Marine Institute (IMARPE) issued a report suggesting the likelihood that the fishery would collapse from economic pressures from overcapitalization of the fleet and the fishmeal processing plants. In 1971, G. J. Paulik described a scenario that combined economic

\*Guano is the droppings from birds such as pelicans, cormorants, and gannets. These birds feed almost exclusively on the anchoveta and would likely perish without them. Guano is rich in nitrogenous and phosphatic matter and is used as fertilizer.



*Pelicans, cormorants, and gannets on island off the coast of Peru. The droppings (guano) of the birds are rich in nitrate for fertilizer. Their sole food is the anchoveta.*

pressures similar to those discussed in the 1969 report with the occurrence of a major El Niño, suggesting the inevitable decline of the anchoveta fishery. His description approximated what actually transpired in 1972-73.\*

Thus the Peruvian anchoveta situation suggests that although in theory there might be many positive uses for a reliable El Niño forecast, in practice its value may be more limited. A further limitation is imposed by disagreements within the scientific community. The survey suggested that even with a reliable forecast, there would still be no consensus among scientists about how it might be linked to biological productivity, and in turn, used as an effective management tool. Faced with contradictory views, policymakers might well weigh all opinions equally, in effect cancelling out the input of the scientific community to the decisionmaking process. Despite a constant call for more research to reduce environmental uncertainties, there appears to be little likelihood that such research would lead to unanimity among scientists.

### Major African Coastal Upwelling Regions

Of the five major upwelling regions, three have witnessed the collapse or near collapse of a major commercially exploited pelagic fishery: the Peruvian anchoveta, the California sardine, and the South West African pilchard. With respect to the California sardine industry, the controversy continues as to whether fluctuating environmental conditions or heavy fishing were primarily responsible for its collapse. The literature on the growth and decline of this fishery is substantial and still expanding. The South West African (Namibian\*) pilchard decline is also under scrutiny. It has been suggested recently that scientific information was available that might have prevented the collapse, but that industry and government officials downplayed this scientific input in favor of economic considerations. The South West African fisheries is a multispecies one, making analysis of the situation more complex. Yet debates similar to those concerning the demise of the California sardine and the Peruvian anchoveta are beginning to surface.

What is the situation in the other two major upwelling areas? Both are in African waters, one off

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\*After the 1973 low catch of 1.8 million metric tons (MMT), the fishery recovered somewhat to a level of 4 MMT, only to collapse again to less than 1 MMT in 1977. In 1979, catches included about 1 MMT each of anchoveta and sardine, the latter increasing in number with the decline in anchoveta population.

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\*Namibia is the name given to South West Africa by those (including the United Nations) seeking to gain its independence from the Republic of South Africa.



the coast of the Islamic Republic of Mauritania, and the other off the coast of the Somali Democratic Republic. Are there lessons that might be learned from the experiences of the Peruvian, Californian, and South West African (Namibian) fisheries? To what level and at what rate should exploitation occur, given the current environmental uncertainties?

Africans expressed concern in 1973 and earlier that there was a high probability that non-African long-distance fishing vessels would overfish local waters before the coastal African countries were technically and economically ready to join in the fisheries. For example, Bayagabona, a Nigerian oceanographer, noted in 1973 that there were already indications "that most of the marine fish stocks in Western Africa [were] being fished at maximum sustainable yield and that some [were] in fact already being overfished." Potential conflicts also exist among African nations themselves because the states with rich coastal resources are among the least populated, such as Mauritania, Namibia, and Somalia. The nations with larger populations and demands for fish products such as the Ivory Coast, Ghana, and Nigeria, are relatively more affluent and developed, but are poorer with respect to commercially exploitable marine resources in their coastal zones.

The establishment of the 200-mile exclusive economic zone combined with the need for economic development has focused attention on the exploitation of coastal marine resources. The fishing industries in the three African countries that border major upwelling areas (Somalia, Mauritania, Namibia) are at different stages of development. Somalia presently has the least developed commercial fisheries, Namibia the most developed, and Mauritania is in between, but considerably closer to the Somali situation. Although in the past Mauritania and Somalia have been viewed as among the poorest countries in Africa with respect to natural land resources, their coastal waters are highly productive and must, therefore, be included in any national inventory of natural resources.

### Mauritania

Mauritania is situated in the Sahara desert with its southern territory extending into the Sahelian zone, and has a population of 1.4 million. The drought in the West African Sahel (1968-73) adversely affected the country's economic development plans by increasing livestock mortality, intensifying rural to urban migration, and accelerating the deterioration of the land's productivity.

Mauritania is often characterized as a poor, coastal desert country with few exploitable resources. Those that it has — iron ore and copper, for example — are subject to fluctuations in the international marketplace. Exploitation of its coastal

waters, considered by many researchers to be among the most biologically productive in the world, is just now emerging as a high priority in Mauritanian economic development plans. Until recently, vessels from more than twenty countries fished this upwelling region, with little economic benefit gained by Mauritania. For example, although the government derived some benefit through licensing arrangements with foreign vessels, in several instances the fees were not paid by vessels that chose instead to "pirate" their catches or to exploit adjacent waters where fees were lower.

Mauritania's interest in its coastal fisheries was heightened by a recent French report that assessed the value of the annual catch at about \$2 billion, noting that only about 4 percent goes to Mauritania. These conditions may be changing, however, as Mauritanian officials turn their attention toward financing and developing their fisheries. Authorities have requested funds from the international community (both private and government) for trawlers, training, fish processing factories, and storage facilities, and for the expansion of port facilities at Nouadhibou. Officials also have increased licensing fees, for example, for foreign factory ships, and are campaigning for foreign vessels to process their catches in Mauritanian factories.

This is a very exciting but crucial time for those involved in the planning and development of fisheries-related projects in Mauritania. Foreign companies recently have begun to join Mauritania in developing its national fishing industry, and Mauritania is giving these firms incentives, such as the right to expatriate profits, and tax breaks. It is precisely now, as the demands for heavy capital — for fleets and factories — are being voiced, that examples of the growth and development of fishing industries in other developing countries that border strong coastal upwelling regions need to be examined for lessons on what might and might not be done.

### Somalia

Somalia is strategically located on the Horn of Africa, and has one of the highest percentages of nomadic populations in Africa. It, too, is a coastal desert country with biologically productive, unexploited, coastal upwelling. Its population depends primarily on resources derived from the land, such as agriculture and livestock.

In the early 1970s and culminating in 1974-75, Somalia was plagued by drought; about 20,000 people and more than a million animals died. Hundreds of thousands of Somalis migrated to refugee camps. The impact of this natural disaster prompted the government to take advantage of these social dislocations to pursue its plans to convert some of these pastoralists to farmers. In



# The Change from



*The town of Baraawe, where the largest fishing cooperative is located.*

*Inset: Women mending nets at Baraawe.*



*New houses for resettled nomads in Badey with traditional nomadic huts in background.*

# *Nomad to Fisherman in Somalia*



*Truck belonging to Badey cooperative on three-day journey to Mogadishu to deliver load of dried fish.*



*Fish being dried at processing plant in Baraawe.*



*Boats used for fishing at Baraawe cooperative.*

**All Somalia photos by Jan M. Haakonsen**





*Lack of port facilities requires fishermen to anchor their boats away from shore.*

addition, about 15,000 of the 120,000 or so destitute refugees were resettled in four fishing villages along the southern coast, three of which were established specifically for the project. This project was the first phase of a long-term economic and social development program designed to exploit the coastal marine resources of Somalia for local consumption and for export to neighboring countries. These artisanal fishing efforts would complement the developing commercial fishing industry based on the building up of a fleet of trawlers. As noted recently by Haakonsen, "The change from nomadic pastoralism to sedentary fishing is a major one and, on such a large scale, actually unprecedented in history." In fact, it can be seen as a major social experiment. A Somali official noted that:

*Until 1972, when this Ministry [of Fisheries] was formed, Somalia really had no fishing industry, despite having the longest coastline of any independent African country. So the very fact that we've got these nomads to go down to the sea to fish at all is an enormous achievement. I'm sure our investment is going to pay off. Then, twenty years from now fisheries are going to be making a very significant contribution to Somalia's economy.*

The government-sponsored multidisciplinary team that studied the feasibility of fishing village projects concluded that:

*The problem with the fisheries development in Somalia is that nobody knows the extent of the*



*Weighing the catch at Illig, near Badey.*



resources available for exploitation. . . . As part of the renewed interest by the Somali government for sea resource utilization, we proposed that a thorough study of the seas be undertaken as a prelude to any developmental ventures in this field.

If these fishing villages are successful, it will in all probability mean increased exploitation of their coastal living marine resources as demands increase in domestic and export markets. As fisheries management experts have noted for other fisheries, a major factor that adversely affects fisheries productivity in the long run is excess capacity of fleets and factories. As John Gulland, a fisheries expert, often maintained, it is wiser (and easier) to prevent the excess capacity from being developed until more is known about the fisheries than it is to remove such excess capacity after it has been determined that it has impaired the biological productivity of the fishery. This is clearly one of the messages that Somali and Mauritanian planners can see from an assessment of the Peruvian situation.

### A Look Ahead

The situation in Peru should be of interest not only to Peruvians, but also to policymakers in countries seeking to attain higher levels of development through the exploitation of their own coastal marine resources, such as Somalia and Mauritania. Viewed in light of the California sardine and the South West African pilchard declines, Peru's situation suggests that over-capitalization of a fishing industry must be avoided; that lower levels of exploitation must be made acceptable until environmental uncertainties can be reduced; that fishing for export should not be considered a country's primary means of development; and that more scientific information, even of better quality, might not ensure that the right decisions will be made.

It is apparent that Peru's anchoveta needed an advocate to counter the challenges of those who favored all-out commercial exploitation. Given the environmental and biological uncertainties in coastal upwelling areas, high levels of exploitation must be avoided to protect the marine resources in such regions until those uncertainties are reduced. From the Peruvian example, it is evident that the costs associated with social, economic, and political dislocations caused by the collapse of a fishery could prove to be greater than the temporary benefits derived from overexploitation based primarily on short-term economic interests.

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# Submarine Hydrothermal Ore Deposits

by Michael J. Mottl

"Ores are rocks and minerals that can be recovered at a profit," according to a popular textbook on economic geology — Park and MacDiarmid's *Ore Deposits* (1964). Using this economic criterion, few of the hydrothermal deposits discovered on the seafloor in recent years could be classified as ores because they lie beneath several thousand meters of seawater, which makes their recovery prohibitively expensive. Nevertheless, some deposits are large and rich

*Figure 1. A row of chimneys on the East Pacific Rise at 21 degrees North with multiple vents spouting hot water. Black or white "smoke" forms on mixing. Black smokers are hottest, up to 350 degrees Celsius. Inset: Iron pyrite, silver sulfide, and other minerals glitter in rock retrieved at 21 degrees North. (Photo by Emory Kristof. © National Geographic Society)*



enough to be exploitable, and those that are not promise to be profitable in another way by increasing our understanding of how hydrothermal ores form so that we can locate them more easily in the future.

The study of submarine hydrothermal deposits was considerably advanced in 1979 with the discovery of hot springs on the East Pacific Rise at 21 degrees North. Unlike the warm springs discovered a few years ago on the Galápagos Spreading Center (see *Oceanus*, Vol. 20, No. 3, p. 35), these springs are *hot*! They are venting water at temperatures as high as 350 degrees Celsius at velocities of several meters per second, and are precipitating prodigious quantities of sulfide ore, minerals rich in copper, zinc, and iron. The precipitates form chimneys around the individual vents that spout black or white smoke composed of precipitated crystals of sulfides and other minerals (Figure 1). The discovery is easily the most exciting and significant in this field since the discovery of the Red Sea hot brines and metal deposits (see *Oceanus*, Vol. 22, No. 3, p. 33).

### Hydrothermal Ore Deposits

Hydrothermal refers to hot water: hydrothermal deposits are deposits that have formed by chemical precipitation from hot solutions, the principal constituent of which is water. There are many different types of hydrothermal ore deposits, formed in a wide variety of environments and under a wide range of conditions. Together they represent one of the most economically important classes of ore deposits, yielding much of the world's supply of copper, zinc, lead, silver, gold, tin, molybdenum, and other metals. All hydrothermal ore deposits have five components that contribute to their formation: 1) a source for the ore metals; 2) a source for the water that dissolves the metals and later precipitates them, concentrating them in the process; 3) a source of heat; 4) a system of permeable pathways through which the water flows from source to the site of deposition; and 5) the site of deposition. In addition, the ores must be deposited in a setting that allows them to survive (for perhaps millions of years) the ravages of weathering, erosion, and other processes that would tend to disperse the metals. Variations in these five components, along with differences in the physical and chemical conditions experienced by the hot solution as it travels from its source to the site of deposition, account for the great variety of hydrothermal ore deposits exploited today.

The submarine environment provides a unique combination of components for the formation of hydrothermal deposits. By far the most abundant source of heat in this setting is that associated with the formation of new oceanic lithosphere along the mid-ocean ridge system, where the seafloor is spreading apart and basaltic

magma wells up from deep within the earth to form new ocean crust (see *Oceanus*, Vol. 17, No. 3). The new crust becomes highly fractured as a result of the tensional forces that pull the lithospheric plates apart. Seawater percolates down through the fractures, becomes heated through contact with the hot rock, and begins to react with it, leaching metals from the rock. The heated seawater, now chemically modified and carrying dissolved metals, is less dense because it is hot, and so tends to rise. It ascends to the seafloor, exiting as submarine hot springs whose waters mix with the ocean bottom water. Thus, for submarine hydrothermal deposits, the ore-forming solution is usually modified seawater, the source of metals is the rock of the ocean crust, and the site of deposition is on or within the seafloor. This combination of circumstances has and is producing a variety of hydrothermal deposits on the seafloor, as well as a number of economically important analogues that have found their way onto land, where they are being mined.

### Seawater as an Ore-forming Fluid

The concentrations of ore metals in most natural waters are extremely low, and in normal seawater they are especially so. In fact, concentrations in seawater are so low that simply measuring them accurately has been one of the most difficult problems in marine chemistry during the last 30 years. For example, if one makes artificial seawater in the laboratory from the high-purity "reagent grade" chemicals used by chemists, it will have 100 to 1,000 times the concentration of heavy metals found in natural seawater!

In order for seawater or any other natural water to become an ore-forming fluid, some minimum concentration of ore metals in solution is required. This is because a metal deposit must be fairly large before it becomes profitable to mine. The minimum size for a deposit to be considered ore is an economic question. The total tonnage of ore in a given deposit depends on how long it took the deposit to form and how fast the hydrothermal solutions were able to transport metals to the site and deposit them there. The latter depends, in turn, on the flow rate of the hydrothermal solution, its total concentration of dissolved metals, and the efficiency with which the metals were precipitated as the solution passed through the site of deposition.

For seawater to become an ore-forming fluid, its ore metal concentrations must be increased by a factor of about 20,000 or more. As stated earlier, the most abundant source for these metals is ocean crust. The problem is to get the metals out of the rock and into the seawater, and to keep them there at high enough concentrations until they can be precipitated in a restricted locality. Laboratory experiments on the solubilities of various ore

minerals and metals show us that there are three principal ways to increase the concentration of metals in an aqueous (water-rich) solution in contact with rock — increase its temperature (and pressure), increase its salinity, or decrease its pH, that is, make it more acidic. The first two of these methods are known to be important for submarine hydrothermal deposits; the third is an intriguing hypothesis awaiting confirmation in a natural setting.

The temperatures reached by seawater circulating through newly formed oceanic crust at a mid-ocean ridge may be estimated in several ways. Rocks dredged from fault scarps in these submarine mountain chains indicate from their chemistry, mineralogy, and oxygen isotopic composition that they have been altered by seawater at temperatures ranging from a few degrees to 600 degrees Celsius, with the bulk of the high-temperature alteration occurring at 200 to 300 degrees Celsius (see *Oceanus*, Vol. 19, No. 4, p. 40).

The first submarine hot springs discovered along a mid-ocean ridge, those at the Galápagos Spreading Center, were emitting water at only 20 degrees Celsius, but the chemistry of this water indicated that it had reacted with basalt at 350 to 400 degrees Celsius (Corliss and others, 1978; Edmond and others, 1979). Then came the discovery of the 350 degrees Celsius springs on the East Pacific Rise; the chemistry of this water is presently being analyzed in John Edmond's laboratory at the Massachusetts Institute of Technology (see *Oceanus*, Vol. 23, No. 1, p. 33).

Figures 2 and 3 show the concentration of iron and manganese in seawater that reacted with basalt for many months in laboratory experiments at high temperature. Also shown are data from the seawater-fed hot spring at Reykjanes, Iceland. Iron and manganese, while less important as ore, are much more abundant in both rocks and solution than are copper, zinc, and other ore metals. All of these metals can be expected to show the large increase in concentration with temperature (and pressure) shown in the figures. Note that the largest increase occurs above 350 degrees Celsius. For altered seawater solutions such as these that have normal salinity and are neither strongly acid nor strongly alkaline, 350 degrees Celsius represents the *minimum* temperature at which seawater is likely to become an ore-forming fluid.

Compared to the solutions responsible for most known hydrothermal ore deposits, seawater is quite dilute, having only 3.5 percent total dissolved salts. Typical ore solutions, as deduced from studies of minute amounts of solution trapped in ore minerals, range in salinity from 3 to 50 percent. The second way to turn seawater into an efficient metal-transporting agent is to increase its salinity. This mechanism is largely responsible for producing the only true hydrothermal ore body

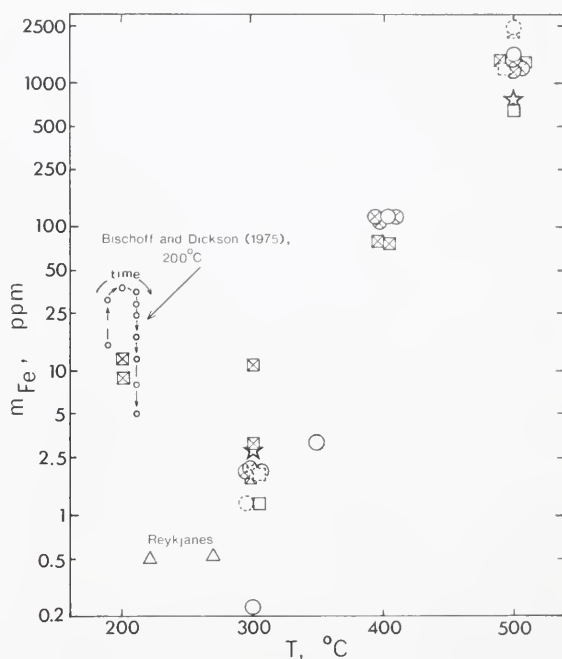


Figure 2. Concentration of iron in solutions produced by reaction of seawater with basalt in laboratory experiments and in the geothermal system on the Reykjanes Peninsula of Iceland (from Mottl and others, 1979).

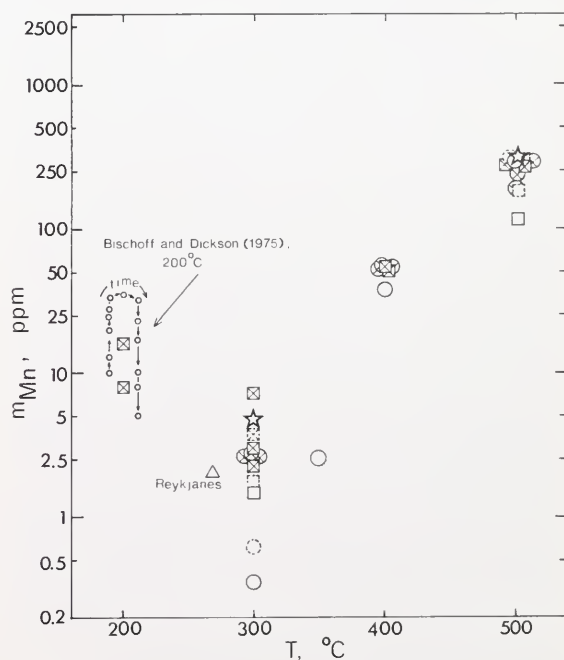


Figure 3. Concentration of manganese in solutions produced by reaction of seawater with basalt in laboratory experiments and in the geothermal system at Reykjanes, Iceland (from Mottl and others, 1979).

discovered so far in the oceans: the deposits in the Atlantis II Deep and in other nearby basins along the spreading center in the Red Sea. As elsewhere along the mid-ocean ridge system, the source of the hydrothermal solutions is seawater, the heat is derived from the seafloor spreading process, and the metals are leached from the crustal rocks. What makes the situation in the Red Sea unique is that the hot, circulating seawater encounters not only volcanic rock during its subterranean travels, but also salt — huge deposits of it, several kilometers thick. These deposits of predominantly halite (NaCl, common table salt) formed when the Red Sea was younger and narrower than it is today. The salt deposits formed by evaporation of seawater in the long, narrow new ocean basin when its outlets to the rest of the oceans were constricted or closed.

Halite is extremely soluble, especially in hot solutions, so these deposits are readily dissolved into the circulating seawater, increasing its salinity to about nine times that of normal seawater. The resulting hot brine has a much greater capacity for transporting ore metals in solution because most of these metals readily combine with the chloride ion,  $\text{Cl}^-$ , in solution to form highly soluble neutral or charged complex ligands, such as  $\text{FeCl}^+$ ,  $\text{CuCl}^0$ , and  $\text{ZnCl}^0_2$ ; these complexes form in greater abundance at higher temperatures and chloride concentrations. Thus, the Red Sea hot brines contain high concentrations of manganese, iron, lead, zinc, copper, cobalt, silver, and other metals.

The third method for dissolving high concentrations of metals in seawater is by lowering its pH, which is the same as raising the hydrogen ion ( $\text{H}^+$ ) activity in solution. As anyone knows who has spilled battery acid on his car, metals tend to dissolve readily in acid ( $\text{H}^+$ -rich) solutions. Experiments at Stanford University four years ago led to a startling discovery: ordinary seawater, when heated to high temperature (greater than 250 degrees Celsius), has a built-in mechanism for becoming a highly acid hydrothermal solution (Bischoff and Seyfried, 1978). As temperature increases, seawater becomes saturated with and precipitates a previously unknown and as yet unnamed mineral containing magnesium, sulfate, and hydroxyl ( $\text{OH}^-$ ) ions. Magnesium and sulfate are two ubiquitous constituents of sea salt, whereas the hydroxyl ion comes mainly from the water itself:  $\text{H}_2\text{O} = \text{H}^+ + \text{OH}^-$ . This reaction coupled with removal of  $\text{OH}^-$  from solution into the new mineral produces free  $\text{H}^+$ , making the hot seawater very acid (pH 3.5 at 350 degrees Celsius). Such an acid solution is very corrosive to the surrounding rocks and readily attacks them, leaching metals into solution. This reaction with the rocks tends to consume the  $\text{H}^+$  and also to convert the  $\text{Mg-OH-SO}_4$  mineral into common  $\text{Mg-OH-silicate}$  minerals, such as clays. Whether the hot seawater remains acid depends on the relative rates of the

$\text{H}^+$ -producing and  $\text{H}^+$ -consuming reactions. These depend, in turn, on how fast seawater flows through the submarine hydrothermal system, compared with how fast it reacts with the rocks it flows through. If flow rates are more rapid, then extremely metal-rich hot spring solutions can be produced (Figure 4).

Although such highly acidic hot springs have yet to be discovered, plans are being formulated to explore the area where they are most likely to occur: along the East Pacific Rise south of the equator. This area of the seafloor contains the most extensive hydrothermal deposits known to exist in the oceans. The deposits are predominantly iron and manganese oxides that have accumulated four to thirty times faster than the normal rate for the deep oceans. Mixed in with normal deep-sea sediment, they are a few meters to a few tens of meters thick and extend from about 10 to 30 degrees south, covering an area of 625,000 square kilometers.

### The Seafloor as a Depositional Environment

An ore deposit is by its very nature a *concentration* of metals. Even most ore-forming solutions have lower concentrations of metals than the rocks from which the metals were leached. Thus, most of the real concentrating gets done at the site of deposition by processes that remove the metals from solution. If an ore deposit is to be formed, these processes must operate efficiently and over a restricted area, removing metals from a very large volume of solution as it passes through. Otherwise, in the absence of a depositional environment with suitable characteristics, the solution will simply distribute the metals over a wide area once again.

The common feature of depositional environments for hydrothermal ore deposits is their ability to produce a rapid and drastic change in those properties of the solution which keep the ore metals dissolved in the first place — temperature, pressure, salinity, and pH. Another important property is the degree to which the solution is oxidized. Rapid and drastic changes in these properties can cause the metals to be “dumped” from solution, whereas more gradual changes cause them to be precipitated slowly over a larger area. Thus, slow cooling of a hydrothermal solution as it ascends toward the surface, by loss of heat to the surrounding rocks, is less likely to produce an ore deposit than is the rapid cooling that would result from a sudden pressure drop, or from mixing with another, cold solution. As for a sudden change in pH, this is most likely to occur when the hydrothermal solution encounters either another, more alkaline solution, or a different type of rock, such as a calcareous marine sediment, and reacts with it. A third mechanism for raising pH is boiling,



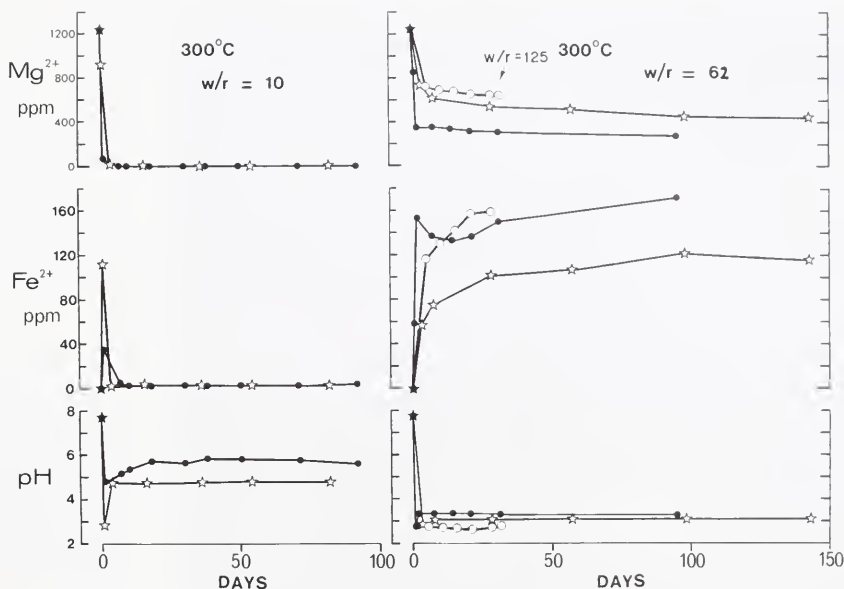


Figure 4. Concentrations of magnesium and iron and pH with time in solutions from five experiments reacting seawater with basalt. The two experiments on the left used low water/rock ratios and simulate flow that is slow relative to reaction. The three on the right, at high water/rock ratios, simulate flow that is fast relative to reaction (from Mottl and Seyfried, 1980).

accompanied by loss of acid-forming gases such as carbon dioxide.

A depositional environment must have two other properties if it is to produce an ore deposit — it must be stable and remain in one place long enough for a sizable amount of ore to accumulate there, and the ore must be preserved there after deposition until it can be discovered and exploited.

Most submarine hydrothermal activity is likely to occur along the mid-ocean ridge system. In this setting, boiling is unlikely to occur because of the high pressure from the 2 to 3 kilometers of overlying seawater. Reaction of hydrothermal solutions with marine sediments will be the exception rather than the rule, as sediment is normally very thin or absent altogether on such very young crust. One process for precipitating metals from hydrothermal solutions, however, is virtually inevitable in any submarine setting: mixing of the solution with ocean bottom waters. As hydrothermal solutions are normally hot, slightly acid, and reducing, whereas normal seawater is cold, slightly alkaline, and oxygen-rich, mixing of one with the other produces a drastic and nearly instantaneous change in the chemical and physical conditions in solution. The dramatic result can be seen in Figure 1, which shows the plume formed by rapid, turbulent mixing of a 350 degrees Celsius metal-rich hydrothermal solution with 2 degrees Celsius bottom water on the East Pacific Rise. The black smoke consists of iron, copper, and zinc sulfide minerals that have precipitated on mixing.

### Submarine Hydrothermal Deposits

To date, no submarine hydrothermal deposit has been sufficiently studied that all components contributing to its formation are known. Nevertheless, the data at hand suggest some intriguing relationships among known deposits along mid-ocean ridges, pointing out the importance of special situations in producing and preserving large deposits. A review of known deposits illustrates this:

*East Pacific Rise, 21 degrees North.* The spectacular discovery in 1979 of hot springs near the mouth of the Gulf of California was presaged by the finding the previous year of spire-like chimneys composed of ore-grade zinc, copper, and iron sulfide minerals in the same locality (CYAMEX, 1979). These deposits were discovered by the French submersible *Cyana* during the joint French-American-Mexican CYAMEX expedition, and were associated with extinct hydrothermal vents. When the RISE expedition returned in 1979 with the submersible *Alvin*, operated by the Woods Hole Oceanographic Institution (WHOI), and found the active vents, it was learned that *Cyana* had missed them by at most a few hundred meters, a fine example of the difficulties of search in the deep sea!

All of the active vents discovered occur along a very narrow zone, 100 to 200 meters wide, close to the axis of the spreading center. The RISE expedition observed 25 temperature anomalies associated with active vents over a 6-kilometer-long



*Figure 5. Warm water vents on the East Pacific Rise at 21 degrees North are similar to those found along the Galápagos Spreading Center. Water at about 20 degrees Celsius flows out from among the rocks, supporting a diverse biological community, including crabs and foot-long clams.*

segment of the ridge crest (RISE, 1980). The vents range from the very high-temperature type (Figure 1) in the southwest to much cooler, Galápagos-style vents (Figure 5) in the northeast. The cooler vents are emitting water at 23 degrees Celsius or less and are surrounded by diverse colonies of unusual marine life, including giant clams and tubeworms, crabs, limpets, and an eel-like fish, which depend upon the chemically nurtured bacteria that grow in the vents for their food source. The very high-temperature vents, by contrast, are too hot for living creatures, but even they are quickly colonized in their cooler regions by worms, crabs, and eel-like fish.

The most distinctive features of the high-temperature vents are the chimneys. Most of the chimneys are a few meters tall, but some are as high as 10 meters. They are composed almost entirely of sulfide minerals often arranged in concentric zones (Figure 6), with minor amounts of sulfate and silicate minerals and silica. The chimneys are spaced a few meters apart within elongated vent fields, and typically rise from a mound composed of debris broken from the chimneys themselves. These mounds rest directly on basalt, as there is little or no sediment on such young crust (less than 20,000 years old). The chimneys are spouting either "black smoke," composed of sulfide minerals, or "white smoke" composed of pyrite (iron sulfide), barite (barium sulfate), and silica.

While these deposits are certainly ore-grade (up to 50 percent zinc, 6 percent copper, 0.05 percent silver) and are forming in spectacular fashion, they are not large or extensive. Forming as they do on the open seafloor, they are immediately subject to oxidation and partial dissolution. Exposed to oxygen-rich bottom waters, they are unlikely to survive as sulfides beyond the sediment-free limits of the axial valley. Thus, their depositional environment is favorable to formation of a small deposit, but not to its preservation.

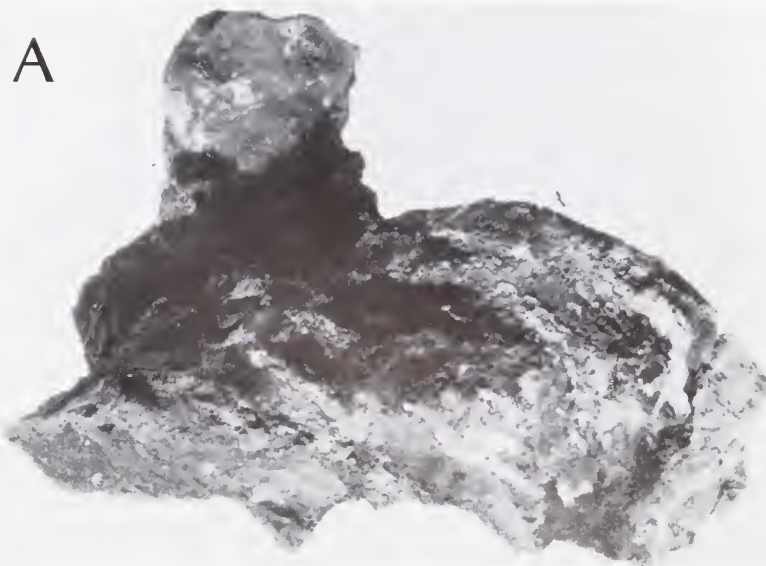
Of greater interest as potential ore bodies are the metal sulfides that may be deposited *within* the seafloor in this setting. Observations made from *Alvin* on a return trip in November, 1979, indicate that vents with temperatures of 350 degrees Celsius are depositing both copper and zinc, whereas vents at 273 and 295 degrees Celsius are depositing only zinc. For the latter vents, copper is probably precipitating within the crust as the solutions cool during ascent. Equally intriguing is the possibility that the Galápagos-style vents in this locality are much cooler than the "smokers" because they have mixed with cold seawater *within* the crust, at shallow levels, rather than above it in the bottom waters. This would shift the site of ore deposition to a more protected location. The chemistry of the Galápagos warm springs suggests that this is indeed happening.

*Galápagos Spreading Center.* No hydrothermal deposits have been recovered from



A

Figure 6. Two views of a chimney from the East Pacific Rise at 21 degrees North. A: Side view of 15-centimeter high chimney, which was spouting hot water at 350 degrees Celsius when sampled in November, 1979. Chimney, at left, protrudes from a base of massive sulfides. B: View of same sample looking upward through chimney. Center of chimney is hollow and is lined with chalcopyrite,  $\text{CuFeS}_2$ . Inner yellow zone is chalcopyrite and pyrite,  $\text{FeS}_2$ . Outer black zone is wurtzite,  $\text{ZnS}$ , and pyrite. White patch near center of photo is anhydrite,  $\text{CaSO}_4$ , and talc, a hydrated Mg-silicate. (Photos by Marjorie Styr) )



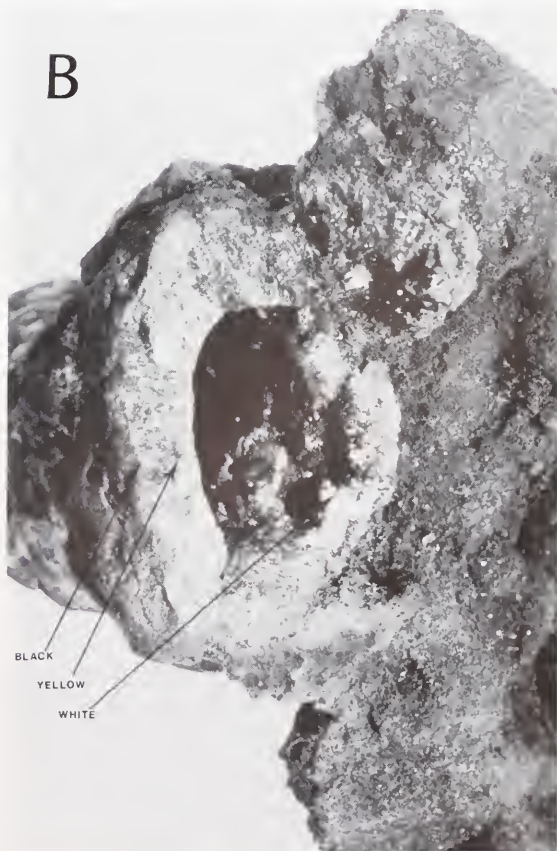
the crest of the Galápagos Spreading Center, where the first warm spring vents were discovered and sampled in 1977. Features that appear to be extinct sulfide chimneys have been photographed but not sampled. Nonetheless, comparison of the chemistry of the warm spring water with that from laboratory experiments indicates that the warm water results from shallow subsurface mixing of cold seawater with a 350 to 400 degrees Celsius, metal-rich hydrothermal solution. Thus, one can imagine the precipitation processes observed on the East Pacific Rise at 21 degrees North occurring *within* the seafloor at the Galápagos, forming a well-protected ore deposit.

Metal deposits, mostly iron silicates and manganese oxides, do occur 25 kilometers south of the Galápagos Spreading Center, where they form mounds protruding from the sediment. Precipitation of the metals here is mediated by reaction of the hydrothermal solution with normal marine sediments, as the solution emanates from long fractures in the underlying basalt.

*Mid-Atlantic Ridge.* The best-known deposit here is from the TAG hydrothermal area at 26 degrees North, discovered in 1970 by the Trans-Atlantic Geotraverse project. This deposit is pure manganese oxide. The TAG area may be similar to the Galápagos in having extensive shallow subsurface mixing. The chief unknown in this area is the temperature, and therefore metal content, of the hydrothermal end-member solution involved in mixing. If high, an ore deposit may be forming within the crust here as well. Plans have been made to visit this area with *Alvin* in 1982.

*East Pacific Rise, 10 to 30 degrees South.* These extensive, rapidly accumulating sediments, rich in iron and manganese oxides, have already

B





been mentioned in discussing seawater as an ore-forming fluid. The remarkable thing about these deposits is their great volume, which implies a much larger input of hydrothermally-derived metals than elsewhere along the mid-ocean ridge system. Whereas the sulfide deposits at 21 degrees North on the East Pacific Rise are highly localized, these deposits blanket about half of the total area of new ocean crust along this part of the ridge, which is spreading at an abnormally rapid rate. Presumably the high metal input is related to the fast spreading rate, but exactly how or why is not known. Perhaps the hot springs here, none of which have yet been discovered, are hotter or more acidic than elsewhere.

Another interesting question concerns the mineralogy and chemistry of the deposits. Are sulfides forming here, as at 21 degrees North, which are then oxidized to oxides and hydroxides by prolonged contact with ocean bottom waters? If so, why are these deposits so relatively poor in zinc and copper? Do rich deposits of zinc and copper lie on and within the crust in this region? If so, they may be analogous to the copper deposits on Cyprus. These deposits are among the earliest known to have been exploited — they were worked for copper ore as early as 3000 B.C., and were mined extensively by the Romans for centuries. They are still yielding copper today. The deposits are located within a slab of ocean crust that was thrust onto the land when Europe collided with Africa millions of years ago. Similar deposits occur in Newfoundland, Turkey, and Oman.

**Red Sea.** As the only genuine hydrothermal ore deposit found so far in the oceans, the Red Sea heavy metal deposits deserve special mention. The unusual metal-transporting properties of the hot brines have already been discussed. What remains is to describe the special depositional environment created by these highly saline hydrothermal solutions. These solutions exit from the seafloor at about 100 degrees Celsius, along the floor of deep fault-bounded basins. Although the solutions are hot, they are denser than normal seawater because of their high salinity, and so do not rise and mix readily with bottom waters. Instead, they remain within the deep basins, which are thus filled with dense, metal-rich brines at a temperature of about 56 degrees Celsius. The metals precipitate within the basins, producing sulfide, silicate, and oxide minerals, depending on the local chemical environment within the brines. Because of their density, the brines are able to create a special and unusual depositional environment for the ores. Mining of these ores by a West German firm that will employ giant submarine "vacuum cleaners" is about to begin.

**Manganese Nodules.** The other submarine ores that promise to be mined eventually are manganese nodules, potato-size nuggets of

manganese and iron oxides rich in nickel, copper, cobalt, chromium, and other metals (see *Oceanus*, Vol. 21, No. 1, p. 60). Manganese nodules are not hydrothermal deposits. Rather, they accumulate slowly by chemical precipitation from normal seawater, in regions of the seafloor with slow sedimentation rates. A long-standing controversy, nonetheless, has been whether nodules contain some amount of metal derived from a hydrothermal source. Figure 7 shows that manganese derived from the warm spring vents along the Galápagos Spreading Center is easily detectable in otherwise normal ocean bottom waters. This effect can be seen at least 250 kilometers from the ridge (Bolger, and others, 1973). This kind of evidence has revived the controversy over the source of metals in the nodules, in at least some areas where the nodules occur.

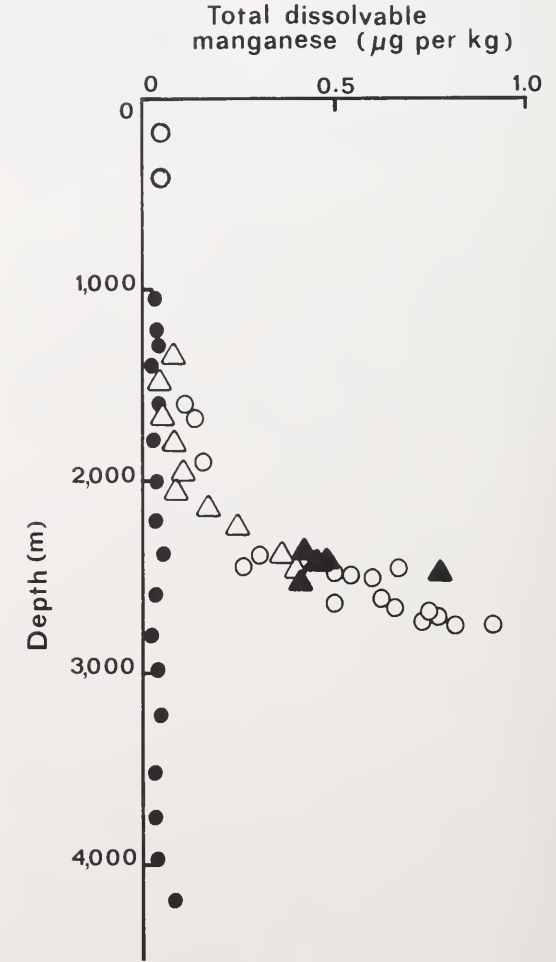


Figure 7. Concentration of manganese, including both dissolved and particulate, in seawater from the open Pacific (closed circles) and from the Galápagos Rift (open circles and triangles) (from Klinkhammer and others, 1977).

*Other Environments.* While most hydrothermal activity in the oceans occurs along the mid-ocean ridge system, this is not the only submarine environment where such processes take place. Two particularly promising non-ridge environments where ore deposits may be forming under the sea are the diffuse spreading centers that create marginal seas behind island arcs, such as the Sea of Japan, and the bases of the volcanic island arcs themselves. While hydrothermal processes here will be similar to those at mid-ocean ridges in most respects, two factors make them potentially different. First, the molten magmas that form and erupt in these environments have a much higher content of water from the earth's interior dissolved in them than do the characteristically dry magmas (less than 1 percent H<sub>2</sub>O) at mid-ocean ridges. Some of this water, which would be acid and metal-rich, may be involved along with seawater in forming metal deposits in these environments. These water- and silica-rich magmas also are more likely to erupt explosively than are mid-ocean ridge lavas, fracturing the hot young rock and allowing ready access for seawater. Second, the more silica-rich rocks formed from these magmas are richer in some metals, notably lead, than are basalts. Thus, ore deposits formed here would be lead-zinc-copper deposits. A noted example of submarine island-arc ore deposits is the Kuroko ores of Japan. Similar ores occur in the Philippine Islands, Fiji, Tasmania, Canada, and possibly Turkey.

### What the Future Holds

The discovery of the East Pacific Rise hot springs has spurred tremendous interest among the oceanographic community. Plans are now being made to launch a four-year, multi-institutional project to explore the East Pacific Rise for additional areas of hot spring activity and ore deposition. The major objective of the program will be to examine the nature of hydrothermal processes along the mid-ocean ridge system from the slow-spreading to the very fast-spreading segments, such as at 10 to 30 degrees South. The project will involve the use of surface ships; deeply towed instrument packages, such as Scripps Institution of Oceanography's Deep Tow and WHOI's *Angus* sled; new high-precision multibeam echo sounding for making highly accurate topographic maps of the seafloor; and ultimately manned submersibles, including *Alvin*. I think it is fair to say that this rewarding field of research is about to experience a veritable explosion of information, which cannot help but improve our understanding of how, where, and why an important class of metallic ore deposits forms.

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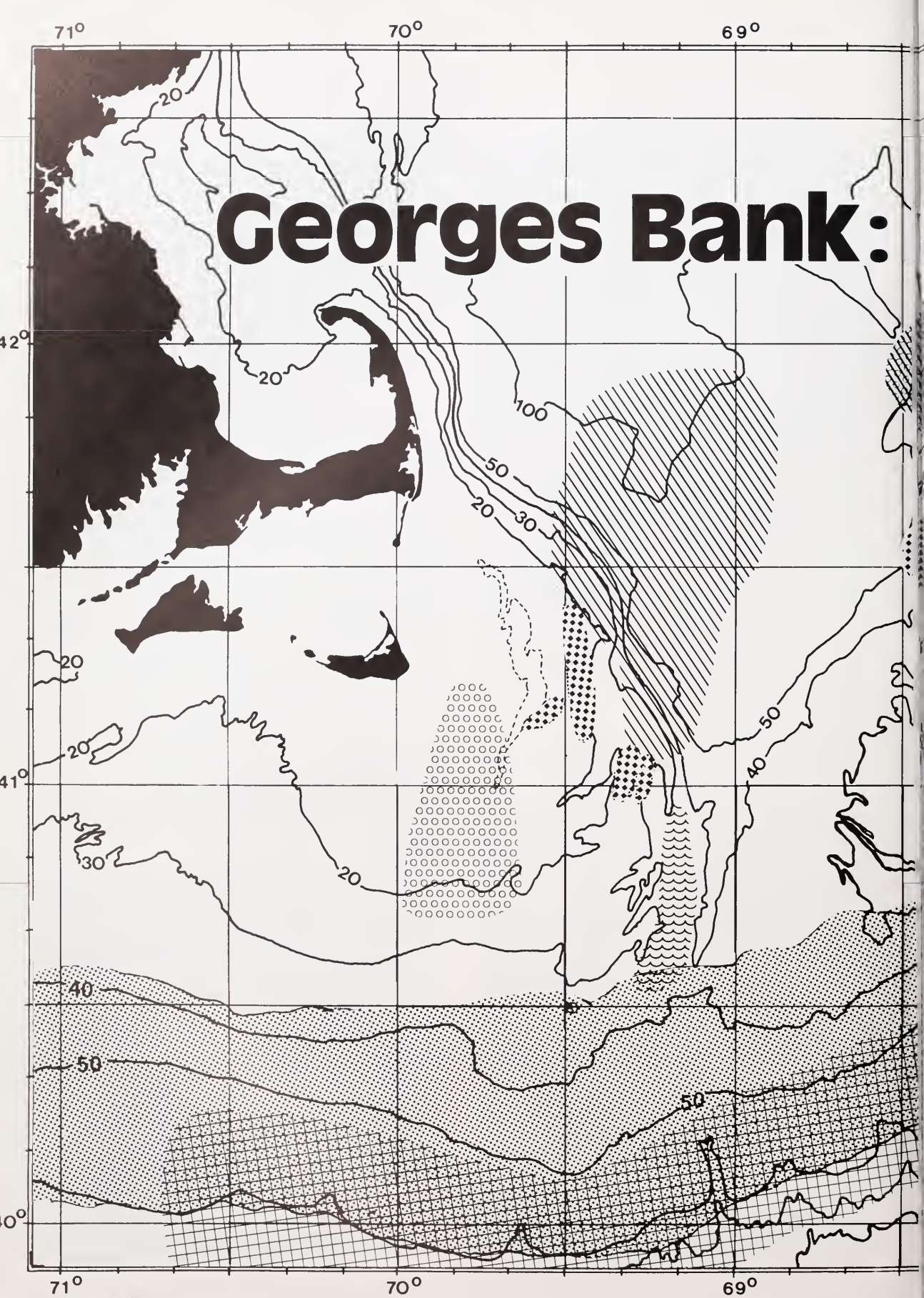
### Acknowledgment

The writing of this article was supported by a grant from the National Science Foundation — OCE 78-19455 — to the Woods Hole Oceanographic Institution.

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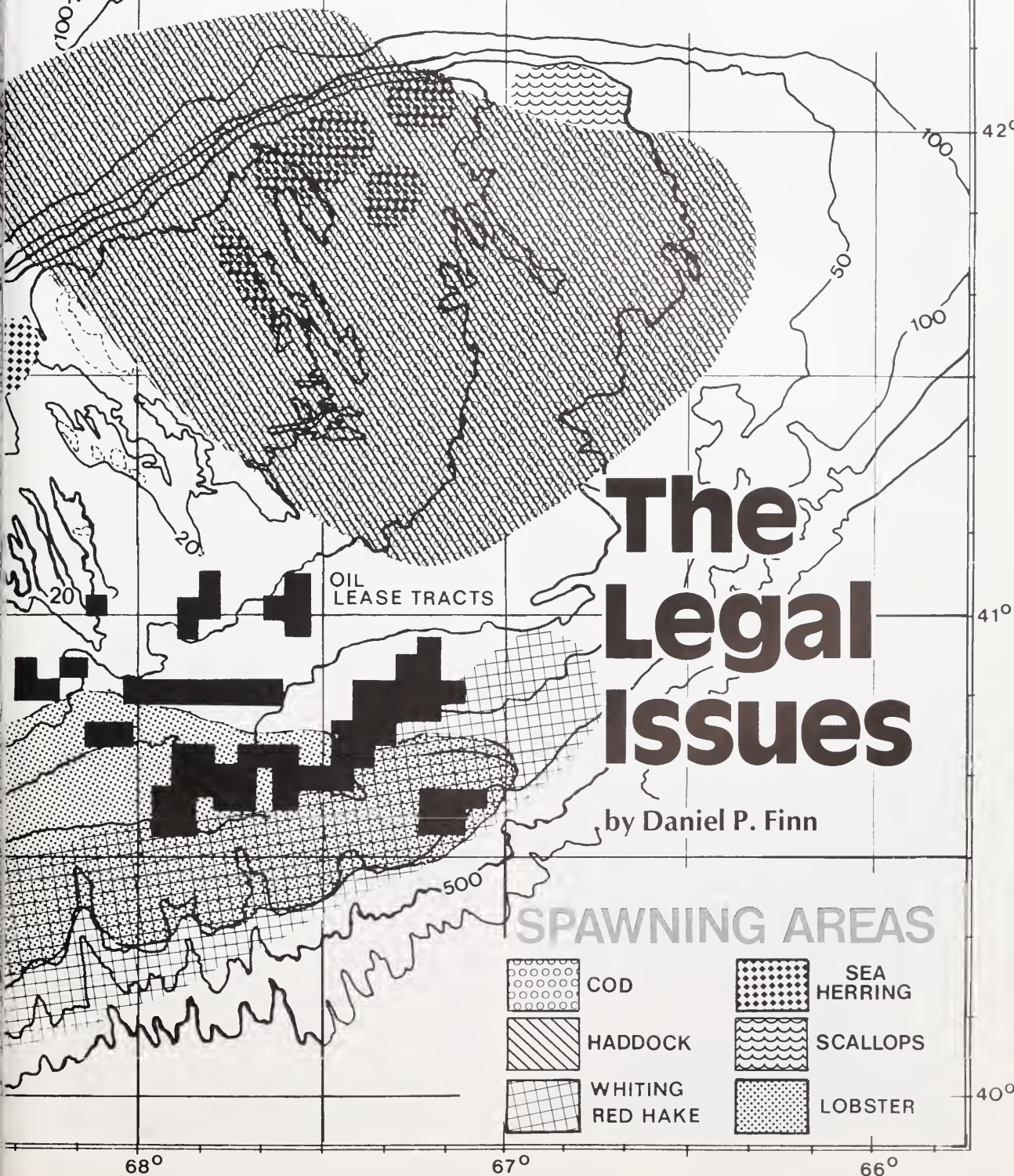
# Georges Bank:

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Tracts leased as a result of Lease Sale No. 42, plotted against the spawning areas of major commercial fisheries. Some scientists believe that spills or discharges from oil operations on the tracts could affect the commercial fisheries, especially if the eggs or larvae of these species are exposed to significant pollution by hydrocarbons or other substances associated with drilling. (Based on A. Rieser and J. Spiller, 1980, work in progress)



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On December 18, 1979, the United States Department of the Interior held Outer Continental Shelf (OCS) Oil and Gas Lease Sale No. 42 for Georges Bank, a sale that had been delayed nearly two years because of legal and political difficulties. Bids were accepted on 63 of the 116 tracts offered — each about 22.5 square kilometers in area. In the spring of 1980, bidders filed exploration plans that would allow them to begin drilling. However, further complications will no doubt arise during subsequent stages of the approval process, because of continued consultation between Interior and other federal agencies, review by the states, and participation by the public. For example, additional environmental impact statements (EIS) will be prepared, and further litigation by the states or outside interest groups is also probable.

The lease sale itself generated considerable controversy. It was the first formal opportunity to address the most important issues regarding whether or how oil and gas activities should be conducted on Georges Bank. The location of the tracts offered and the terms and conditions of the leases are significant in determining the effects of such activities. Also, the decisionmaking of the federal agencies and other parties prior to the sale is a good indication of how future decisions will be made.

The sale was held after considerable public disagreement by two federal agencies — the Department of the Interior, which regulates oil and gas activities and conducts OCS lease sales through its Bureau of Land Management, and the National Oceanic and Atmospheric Administration (NOAA), which is responsible for fisheries conservation and management through its National Marine Fisheries Service (NMFS). NOAA also administers the marine sanctuaries program, which allows the Department of Commerce to apply special regulations to protect especially valuable marine areas. Before the lease sale could be held, the Carter administration had to develop a unified position on the terms and conditions of the sale in order to reconcile the views of the agencies and to demonstrate to the public that necessary safeguards had been adopted. As a result, certain potential lease tracts were deleted and an interagency committee was formed to advise Interior on future regulatory measures. Off-site disposal of drilling effluents was not adopted, however, meaning that drilling inevitably would result in a certain degree of pollution. The way this decision was made raises several interesting legal issues.

### Productivity of Georges Bank

Georges Bank is an extremely productive commercial fishery area. Annual landings of fish total about \$168 million, which results in a net economic benefit of more than \$1 billion. Although

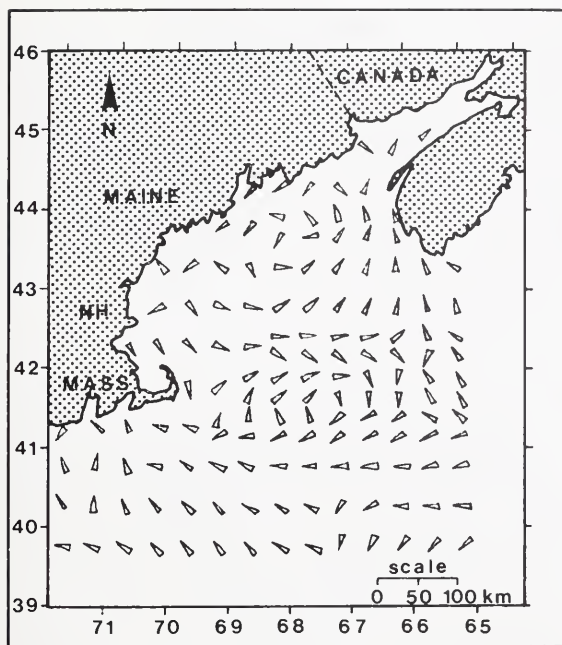
this represents only a small part of New England's economy, the fishing industry is concentrated in a few coastal areas and is an important cultural and social factor in the life of the region. It is projected that with proper management Georges Bank could sustain annual landings of \$229 million.

Hydrocarbon reserves, by contrast, are estimated at 123 million barrels of oil and 870 billion cubic feet of gas, having a net value — less costs of production — of \$588 million. Oil from Georges Bank would probably supply 5 to 6 days of current national consumption. Also, a major gas strike could mean lower prices and greater availability of natural gas for New England.

The productivity of Georges Bank fisheries, which include both demersal species (cod, haddock, pollock, and flounder), and benthic species (lobster, scallops, and quahogs), appears to result from a unique combination of oceanographic conditions in the area, still not fully understood. The area is characterized by an enclosed or semienclosed current gyre, strong vertical mixing, and upwelling. The mixing and upwelling cause considerable nutrient enrichment and therefore a high rate of primary productivity. The current gyre tends to concentrate nutrients and retain plankton, and causes eggs and larvae of commercial species generally to remain in the area of high productivity and develop into strong year-classes.

Several substantive issues have been raised by groups concerned with the threat drilling poses to the fisheries. Some scientists fear that oil being released by routine spills during recovery and transportation and by discharge of pore waters from oil-bearing sedimentary strata (formation waters) during production could lead to chronic pollution of the water column, resulting in fish egg and larvae mortality and alteration of planktonic composition. Some think that because of the intense vertical mixing, discharged oil and other substances, such as drilling muds and cuttings, could become incorporated into sediments or suspended with sediment particles. Some also believe that the current gyre could lead to any large spills being retained within the area, causing damage to developing year-classes of commercial species, since their eggs and juveniles are present over large parts of the Bank during nearly the entire year. On-site discharge of drilling muds and cuttings could result in localized toxic effects on benthic communities, including lobsters, either in areas adjacent to drilling facilities or in areas subject to downslope movement of pollutants — for example, in the canyons that start on the continental shelf edge. These factors have led some scientists to conclude that oil and gas development could have significant effects, both chronic and acute, on the Bank's fisheries productivity.

These unresolved issues are still undergoing extensive environmental analysis and will not be

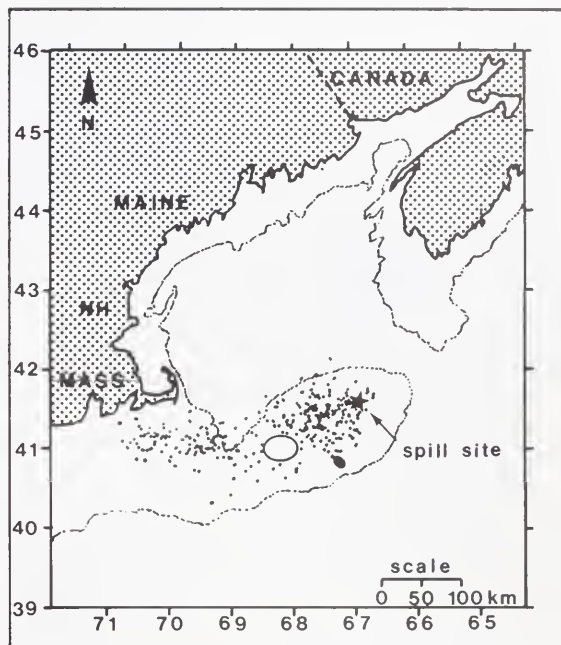


Direction of surface currents during the spring, illustrating the current gyre.

discussed here. Our focus will be on legal questions regarding the sale, including Interior's responsibility to protect fisheries and to consider management alternatives that would be more protective of marine resources, and the effects of NOAA's actions in considering the designation of Georges Bank as a marine sanctuary. While these are not the only legal issues that were raised in connection with Lease Sale No. 42, they provide an unusual glimpse into federal decisionmaking and point up a number of general concerns about the way important decisions affecting marine resources are made.

### History of the Lease Sale

A lawsuit against the lease sale was brought in December, 1977, by the State of Massachusetts and the Conservation Law Foundation of New England, a public interest group. The First Circuit Court of Appeals determined that before proceeding with the sale, the Secretary of the Interior, Cecil D. Andrus, should ensure that the sale would not create an unreasonable risk to fisheries. The Court also commented that the Secretary should consider the possibility of the area being managed by the Department of Commerce, through NOAA, as a marine sanctuary. Under the Marine Sanctuaries Act of 1972, the Secretary of Commerce, in this case Acting Secretary Luther Hodges, is empowered to designate ocean areas as marine sanctuaries to preserve their resources. Within such areas, activities may be directly regulated by the



Projected area affected by a large spill of 34,840 metric tons of oil occurring at the site indicated in early spring after 30 days, plotted against a modeled distribution of fish larvae. The white circle represents the area in which the ambient concentration of hydrocarbons in the water column would exceed 50 parts per billion (ppb). Significant or even complete mortality of fish eggs and larvae could occur in areas of 50 ppb concentration. The dark spot represents the area in which oil would become entrained in sediments.

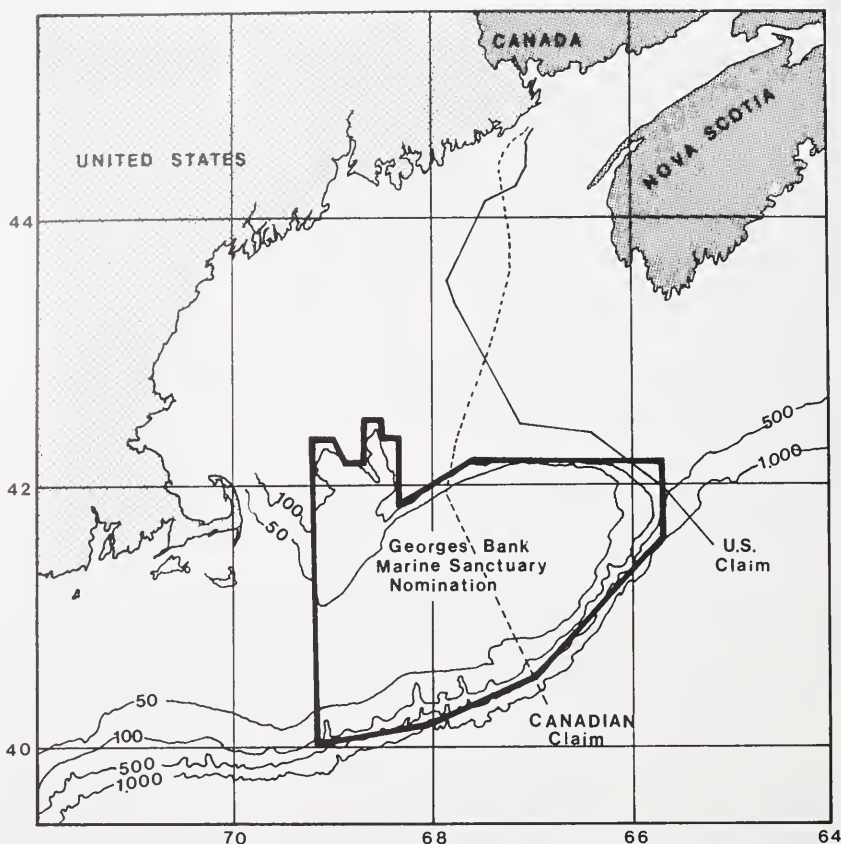
Department of Commerce; in addition, actions proposed by other federal agencies must be certified by Commerce as consistent with the purposes of the sanctuary.

The novelty of the Court's conclusions in the *Massachusetts v. Andrus* case was that henceforth, in deciding whether and how to proceed with this and other lease sales, Interior would have to consider the goals of a statute administered by the Department of Commerce — the Fishery Conservation and Management Act (FCMA) — and even the possibility that Commerce could manage the area as a marine sanctuary with objectives that would likely be different from its own. Interior, after all, is primarily responsible for conducting the government's OCS leasing program, whereas Commerce (through NOAA) is primarily interested in conserving and managing commercial fisheries under the FCMA and protecting unique areas through its marine sanctuaries program.

After the Court's decision, Interior prepared a supplemental EIS that specifically addressed marine sanctuary alternatives and considered fisheries issues in greater detail. Before the draft of this document was released, the Conservation Law



*Boundaries of marine sanctuary proposed by the Conservation Law Foundation. Jurisdiction over the area between the lines marked "Canadian Claim" and "U.S. Claim" is disputed by the two countries.*



Foundation — one of the plaintiffs in the pending lawsuit — petitioned the Secretary of Commerce to designate Georges Bank as a marine sanctuary and manage the area so that the primary federal objective would be fisheries production and conservation; oil and gas activities would be subject to additional regulations to ensure this objective was achieved. Upon receiving the petition, NOAA selected the area as an active candidate for a marine sanctuary. It also provided extremely critical comments on the treatment of fisheries issues and the marine sanctuary alternative in Interior's supplemental EIS, and specifically called Interior's attention to the petition that it had received. NOAA then released an "issue paper" on potential management of Georges Bank as a marine sanctuary and held a series of public workshops in Massachusetts and Maine. Among the alternatives presented in the paper were proposals to limit future oil and gas activities on Georges Bank to the proposed Lease Sale No. 42 area, to delete from the sale those tracts on or near valuable benthic communities, and to impose additional operational regulations, including barging away of drilling muds and cuttings, reinjection of formation waters, and on-site location of pollution control and

containment equipment. NOAA also called for more monitoring of potential biological effects by lessees. Finally, NOAA argued that even if a marine sanctuary were not designated, additional measures would be necessary to make the terms of the sale protective enough and to ensure that Interior continued to carry out its responsibilities properly. These included the formation of a standing interagency committee to oversee operations, and definite interagency and public reviews of various future actions.

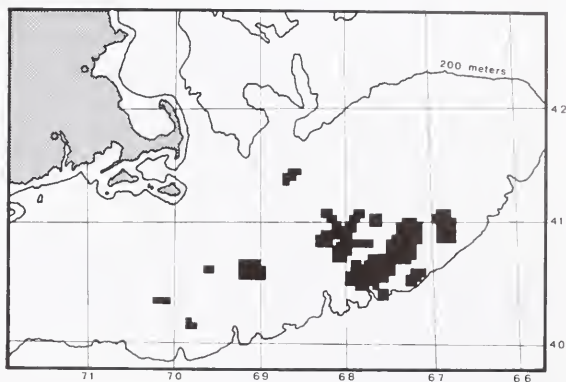
Interior reacted very strongly to NOAA's proposals. Interior claimed that it had primary authority to regulate oil and gas activities and was already obliged to ensure that there was no unreasonable risk to fisheries. Interior indicated that it perceived no basis in fact for believing that NOAA could do a better job than it would. After this exchange, both Interior and NOAA proceeded toward their own decisions about how to manage Georges Bank, while the Carter administration tried to formulate a unified position on the pending lawsuit and the outstanding issues concerning fisheries and the possibility of a marine sanctuary. Finally, on September 21, 1979, Commerce and Interior announced that they had reached an

agreement. NOAA agreed to withdraw Georges Bank from its list of active candidates for marine sanctuary designation, and Interior consented to the formation of an interagency biological task force that could recommend actions to its operational official, the Regional Supervisor of the U.S. Geological Survey (USGS). Interior also agreed to include certain operational measures either as stipulations to the leases or as information to lessees that would give them notice of how their activities would be regulated. (Including regulatory provisions in the leases or in the notice of lease sale is important because the sale of leases creates private property rights in favor of lessees, who have paid the government significant sums — in the case of Georges Bank, in excess of \$800 million — and who will probably invest considerable amounts in exploratory and other activities with the expectation of realizing certain levels of economic return on their leases.)

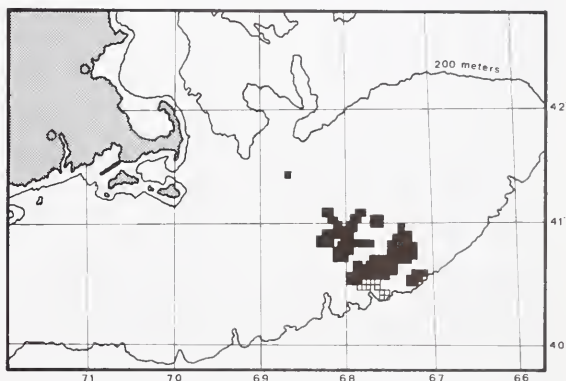
Regardless of its concessions, the agreement has been widely viewed as a victory for Interior. NOAA's issue paper and its comments on Interior's supplemental EIS presented a strong case that certain actions were essential to conserve Georges Bank fisheries. Few of NOAA's recommendations were followed in the agreement, however. The new language of the lease stipulations concerning drilling muds and cuttings and formation waters called only for undefined "safe" disposal of such substances; Interior had never previously exercised its right to require barging and reinjection in similar cases. Lessees were not made subject to extensive biological monitoring requirements; additional monitoring would have to be made largely by federal agencies and others at their own expense. NOAA's recommendation of on-site location of cleanup and contingency equipment was adopted, however, and 12 of the 15 tracts recommended for deletion by NOAA were removed from the sale.

A key issue was the terms of the charter developed by Interior and NOAA to establish an interagency biological task force that was to include officials of these organizations and the Environmental Protection Agency. The task force is not empowered to make binding decisions under its charter. If the USGS Regional Supervisor disagrees with recommendations of the task force, he must state his reasons, however. But three of the five agencies represented on the task force are within the Department of the Interior — the Bureau of Land Management, Fish and Wildlife Service, and USGS. Although any two agencies in the task force may appeal actions of the Regional Supervisor, such an appeal must be based on the Regional Supervisor's failure to follow a recommendation of the task force as a whole — that is, a recommendation adopted by at least three of its members.

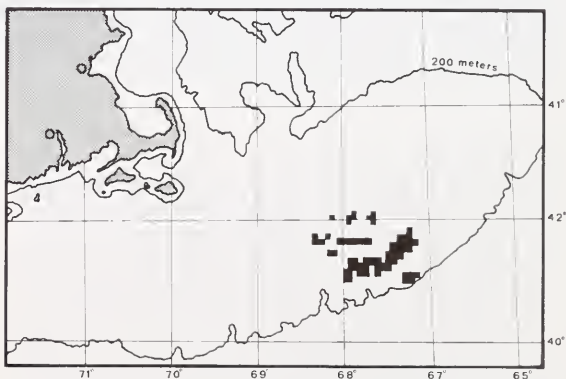
A



B



C



Areas proposed or actually leased in Lease Sale No. 42: (A) the 178 tracts originally presented in Interior's final EIS; (B) the 128 tracts in Interior's supplemental EIS, including the 12 tracts deleted by Interior (open boxes) upon agreement with NOAA; (C) the 63 tracts actually sold.



## Reactions to the Agreement

After Interior and Commerce reached this agreement, the states of Maine and Massachusetts and the Conservation Law Foundation, which had petitioned the Secretary of Commerce for a marine sanctuary, returned to court with additional claims concerning the lease sale as it was then proposed by Interior and the actions that had been taken (or not taken) by NOAA. They claimed that Interior's proposed sale was still defective for failing to protect fisheries and endangered species and to consider the marine sanctuary alternative in its supplemental EIS. They also asserted that NOAA had failed to fulfill its duties by not proceeding with a formal proposal for a marine sanctuary, a proposal that it apparently had felt was desirable and perhaps even essential for adequate protection of the Georges Bank fisheries. NOAA, they asserted, should have at least prepared an EIS so that alternative proposals could be publicly considered. The plaintiffs also claimed that NOAA's failure to proceed further affected the validity of the sale, since had NOAA proposed or designated a sanctuary, Interior's action might have been different.

Hasty judicial proceedings followed, since Interior proposed to hold its sale on November 6, 1979. First, the Federal District Court and then the First Circuit Court of Appeals, hearing the case as *Conservation Law Foundation v. Andrus*, heard arguments right up to the eve of the sale as then proposed, and the First Circuit Court issued its opinion the very morning of the proposed sale. The courts rejected the new contentions of the plaintiffs. They concluded that Interior had adequately addressed the fisheries and marine sanctuaries issues in its supplemental EIS and that NOAA was apparently under no legal obligation to consider further any alternative management plan for the Bank. Although the sale proposed for November 26, 1979, was delayed by last-minute proceedings in the United States Supreme Court, no significant judicial obstacles remained and the sale was finally held on December 18.

## The Marine Sanctuary Issue

The plaintiffs were not successful in pressing their claims that NOAA was obliged to prepare an EIS on a marine sanctuary, and that Interior would have to defer to NOAA's administrative process because it was required to consider the alternative that Georges Bank be managed as a marine sanctuary. The plaintiffs had a difficult case. They were arguing that NOAA had failed to undertake a required action. Regarding the lease sale itself, they were making a complex claim — that Interior was required to await information generated by NOAA, and even to respect the autonomy of NOAA's competing administrative process, since it had to



consider NOAA's actions which could affect how oil and gas operations would be conducted under lease.

Ordinarily, a federal agency is free to proceed with any proposal within its statutory authority provided that it meets all the legal requirements in existence at the time of its action. The original opinion of the First Circuit Court meant that Interior was required to consider the sanctuary. But why should Interior's action be further delayed or even brought into question simply because NOAA was tentatively considering a counter-proposal that could have affected Interior's



*Working Georges Bank in rough weather. (Photo by Nubar Alexanian)*

action? NOAA at this stage had not issued a formal proposal or even a draft EIS presenting definite options. Indeed, NOAA had begun considering a marine sanctuary only at the last minute, in response to a petition submitted by plaintiffs in pending litigation with Interior. Some of the groups on whose behalf the petition was submitted were involved in commercial fishing, and thus were in effect NOAA's "clients" under the FCMA.

Several aspects of the actions taken by both agencies and the nature of the relationships between them nevertheless suggest that there was a legal basis on which the courts could have

prevented the lease sale. First, it is true that it was Interior which was required to consider the marine sanctuary as an alternative to its own proposed action. Nevertheless, NOAA would be required to proceed in a regular and good-faith manner in implementing programs committed to its administration, like the marine sanctuaries program. Second, although NOAA had not made a formal proposal for a sanctuary, it was required by its own regulations to decide within 90 days after having held public workshops whether to proceed with a formal proposal. Third, it is indicated in the public record that NOAA believed the actions



## CHRONOLOGY OF EVENTS RELATED TO THE GEORGES BANK LEASE SALE

June 17, 1975	Department of the Interior (DOI) called for nominations of tracts to be included in proposed Lease Sale No. 42 on Georges Bank. 1,927 tracts were nominated.
Jan. 2, 1976	DOI proposed a list of 206 lease tracts.
Oct. 12, 1976	DOI published a draft environmental impact statement (EIS).
Dec. 7, 1976	DOI deleted 28 tracts because of uncertainty of boundary with Canada, then being negotiated.
Dec. 7-10, 1976	DOI held public hearings on the lease sale and its environmental effects, detailed in the draft EIS.
Aug. 29, 1977	DOI issued a final EIS, in five volumes.
Dec. 28, 1977	DOI deleted 23 tracts to minimize interference with commercial fishing, including trawling and setting and hauling of lobster pots, and to reduce danger of a spill reaching shore.
Jan. 28, 1978	Commonwealth of Massachusetts and Conservation Law Foundation (CLF) and others obtained a preliminary injunction against proposed sale from District Court.
Jan. 31, 1978	First proposed sale date.
Feb. 22, 1979	First Circuit Court dissolved the preliminary injunction but instructed DOI to consider further fisheries and marine sanctuaries issues.
May 10, 1979	CLF and others petitioned the Department of Commerce (DOC) to designate Georges Bank a marine sanctuary.
May 25, 1979	DOI issued a draft supplemental EIS addressing fisheries and marine sanctuaries issues.
June 20, 1979	DOI held public hearings on the draft supplemental EIS.
July 16, 1979	National Oceanic and Atmospheric Administration (NOAA), a DOC agency, submitted comments on the supplemental EIS, criticizing DOI's discussion of fisheries issues and calling attention to CLF's petition.
July 27, 1979	NOAA released an "issue paper" discussing the possibility that Georges Bank could be designated a marine sanctuary.
Aug. 22-24, 1979	NOAA conducted workshops in Massachusetts and Maine about the marine sanctuary.
Sept. 21, 1979	DOI and DOC announced an agreement that would allow the sale to proceed; the Administrator of NOAA indicated his dissatisfaction with the terms of the sale.
Oct. 5, 1979	DOI issued a notice of sale for November 6, 1979.
Nov. 5, 1979	District Court ruled against plaintiffs' new contentions about the duties of DOI and NOAA.
Nov. 6, 1979	First Circuit Court refused to grant a stay delaying the proposed sale; Justice Brennan of the Supreme Court granted a temporary stay, however.
Nov. 9, 1979	U.S. Supreme Court vacated Justice Brennan's order.
Dec. 17, 1979	First Circuit Court rejected appeal from District Court's order of Nov. 5, 1979.
Dec. 18, 1979	DOI held Lease Sale No. 42.

proposed by Interior, and even its own agreement with Interior, were inadequate to protect the Georges Bank fisheries. The terms of the lease sale did not address several substantial concerns raised by NOAA in its comments on Interior's action. Furthermore, the administrator of NOAA, Richard A. Frank, made statements at the time the agreement was announced that indicated he thought the sale as proposed still presented significant dangers to the fisheries and should not have been held.

If NOAA had proceeded with a proposal to designate Georges Bank as a marine sanctuary, its action could have significantly affected oil and gas activities on Georges Bank. It could be argued

therefore that NOAA's failure to proceed with an action that was within its authority and that it apparently believed was necessary allowed Interior to go forward with its lease sale. Thus it appears the courts had grounds for preventing Interior from holding the sale because, if the sale was stopped, NOAA could have fulfilled its statutory responsibilities to protect the fishery resources and to give proper consideration to designating a marine sanctuary. Issuing leases could prevent NOAA from establishing a sanctuary later.

In its formal notice withdrawing Georges Bank from consideration, however, NOAA stated that the agreement it had reached with Interior significantly increased the ability of the existing



*Fishermen's wives protesting lease sale outside White House in Washington, D.C. (Photo by Nubar Alexanian)*

regulatory framework to protect the fisheries and made it more likely that sufficient effort would be devoted to protection, making a marine sanctuary unnecessary. The courts found nothing in the public record that indicated NOAA had abused its administrative discretion, and the First Circuit Court specifically found that NOAA's action was not necessarily inconsistent with its earlier position on the risks of oil and gas operations to the fisheries.

Other aspects of the situation at the time Interior and NOAA reached their agreement present additional grounds for concern, however. To an outside observer, it may appear that there was strong pressure within the Carter administration for NOAA to discontinue considering the sanctuary and to reach an agreement with Interior. NOAA may have received indications within the executive branch that the President would not approve designation of a marine sanctuary. (The statute requires that all marine sanctuaries must be approved by the President). If this is true, then important public interests may have been sacrificed because of the way in which the interagency

agreement between Interior and NOAA was concluded.

Although the Marine Sanctuaries Act expressly provides that the Secretary of Commerce must consult with other federal agencies and secure the approval of the President before designating a marine sanctuary, in this case NOAA stopped well short of the President's desk. NOAA never issued a formal proposal or a set of options that would have permitted full public evaluation of the desirability of establishing a sanctuary. Whatever process of accommodation that was accomplished with the executive branch was carried out informally. The President did not have the opportunity to evaluate the conflict between Interior and NOAA in the context of two well-developed competing proposals. Similarly, Congress, which has an interest in the effective implementation of the laws it has enacted, had no opportunity to oversee the performance of the Department of Commerce or the Administration in implementing the Marine Sanctuaries Act. Finally, because the important issues were submerged and an internal agreement





*Gulf Oil executive talks with State Trooper after being hit in neck with a bag of oil tossed by a protester at Georges Bank oil lease sale on December 18, 1979, in Providence, R.I. (Photo courtesy Providence Journal-Bulletin)*

was reached, the courts reviewed the final decision in terms of technical legal issues about the procedural responsibilities of Interior and NOAA. For all these reasons, public scrutiny and participation were limited and the legitimacy of the ultimate decision was affected. All these factors could have provided a legal basis for preventing the lease sale.

#### **Lessons of the Georges Bank Lease Sale**

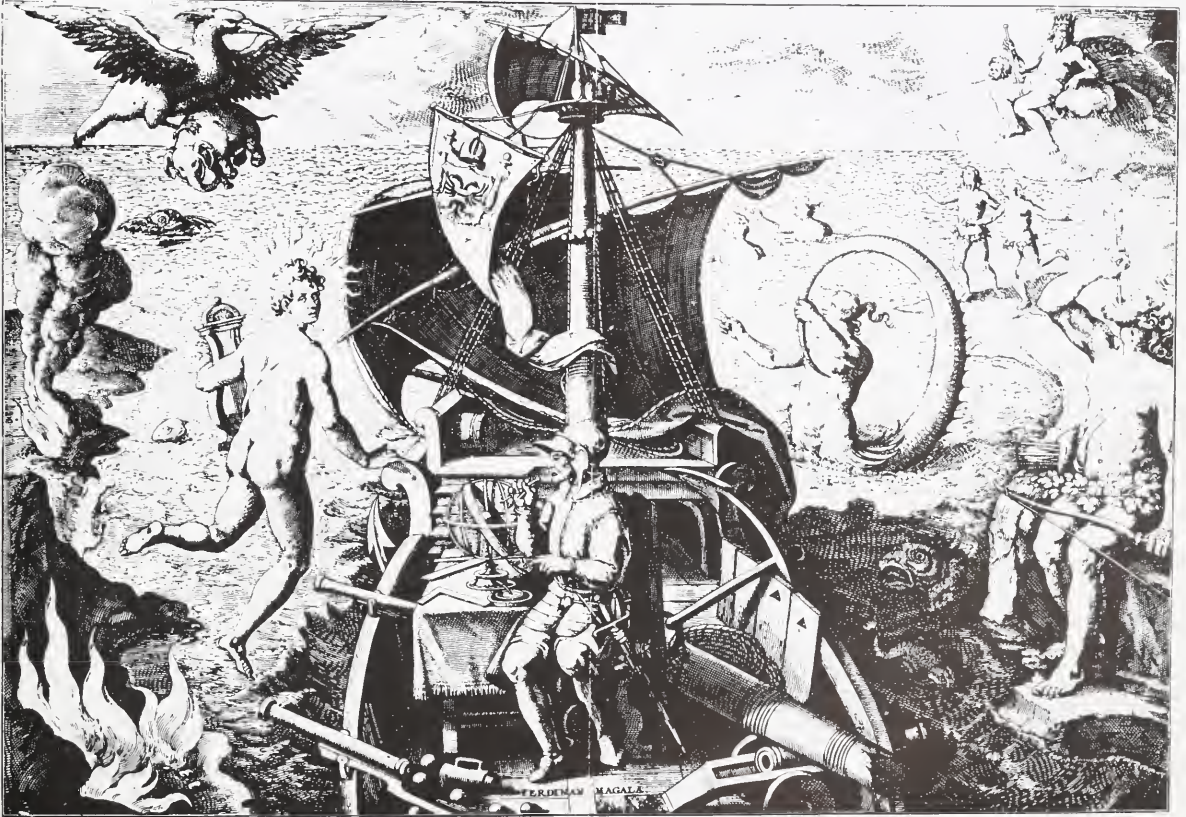
A wide range of views is held among the general public and among scientists and government officials about whether oil and gas activities should be permitted on Georges Bank and how such operations should be regulated. Regardless of one's position, the Georges Bank lease sale raised critical questions regarding how effective and legitimate governmental actions can be achieved in situations where significant marine resources are at stake. It is important to realize that even the way such decisions are made has important consequences for the successful resolution of conflicts between development and conservation interests in marine areas.

Numerous statutes have created overlapping responsibilities among federal agencies often with conflicting missions and different perspectives on how marine resources should be managed. If these agencies fail to conduct their proceedings in an open and well-coordinated manner, significant

questions will be raised about their decisions whatever the final outcome. Although important decisions have yet to be made on how oil and gas operations should be conducted on Georges Bank, the history of the lease sale itself shows that we still have a long way to go in developing institutions that can bear the strain of conflicting pressures. Whatever the ultimate decisions, however, they should be reached in a public and principled manner so that conflicting opinions of fact and value about the wisdom of proposed actions are faced squarely and openly.

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# The Development of Marine Science in Latin America



*Allegorical representation of Magellan's trip around the world. (The Bettmann Archive, Inc.)*

by Francisco J. Palacio

The large contributions to the exploration of the oceans made by the Spanish and the Portuguese about five centuries ago have not been matched subsequently by their descendants. Marine science in Latin America today is generally underdeveloped, impoverished. In most cases, there is no strong national commitment to develop and manage the coastal zone. Education in the various disciplines is minimal — this, in fact, is the case for most scientific endeavors in general. And yet — the potential is tremendous. There is a stirring of interest in the oceans once again, but Latin nations must look not to international agencies and institutions to solve

their problems, but inwardly, to themselves, to their own pool of human resources. The task before them is monumental, but not impossible. Let us briefly review the major contributions of the past, the early events that set the foundations of the present status of the marine sciences in Latin America,\* and touch on some trends, problems, and programs.

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\*The term Latin America is used to include mostly, but not exclusively, the countries of continental Central and South America.



## History

John Murray's superb 1895 historical account of marine investigations prior to the voyage of the *H.M.S. Challenger* recognizes Ferdinand Magellan's deep-sea soundings in 1521 (in the present Tuamotu Archipelago) as the first recorded in the open sea. Magellan's voyage for Spain's Charles V also was the greatest event in the thirty-year period from 1492 to 1522, when Spanish exploration doubled knowledge about the earth, adding a hemisphere to a world that could, indeed, be circumnavigated. But the discovery of new lands to be colonized, natives to be proselytized, species to be traded, and precious metals to be mined, all led Spain to change its maritime interests from exploration to the transport of goods. This was based upon a land economy supported by a lavish use of Indian and Negro labor, the character of which represents an important part of today's problems in Latin America.

Across the English Channel, Drake, the defeat of the Armada in 1585, and the Treaty of London in 1604 opened the doors of the New World to England and Europe in the 17th century. A century later, Captain Cook, Harrison's chronometer, and the sextant opened the Pacific Ocean to the British Admiralty. Less well known is the fact that Spain also explored the Pacific. Alvaro de Mendaña (1567), Fernando de Quiros (1595), Vaez de Torres (1606), and other smaller expeditions stirred by British and French discoveries, contributed significantly to the explorations of the South and North Pacific. Spain's resentment of European intrusion resulted in a policy of secrecy of discovery that contrasts with the numerous publications on the voyages of Cook, La Pérouse, and Vancouver. The diplomatic pressure exercised by greater military strength forced Spain in 1790-95 to give up its claims and settlements to Great Britain. As a result, the world at large did not realize that at the turn of the 18th century, the Iberians had made more charts and maps of the newly discovered regions than any other group of navigators. By then, not only English vessels, but also their maps, language, and literature began to rule the seas.

Although a methodic study of the Peru current was not made until Humboldt undertook one in 1802, Pizarro and his followers were well aware of the force, impact, and vagaries of the current. We owe the discovery of the Galápagos Islands, already known to Inca rulers, to an attempt by Panama's bishop to avoid the current en route to Peru to settle a dispute between Pizarro and Almagro. Early sailing directions were compiled by Cieza de Leon in 1553, and the current was discussed by Father Acosta in 1608, who identified the attributes of El Niño (see *Oceanus*, Vol. 21, No. 4, p. 40). For two centuries, from 1600 to 1800,



Magellan  
(The Bettmann Archive, Inc.)

knowledge of the current was derived from short references in journals and logs. There was a general feeling that the cool water off the west coast of South America was related to the height of the Andes. In the Gulf of Panama, where the Andes are relatively low, the waters were warm, whereas off Peru, where they are high, the water was cool. This, and cloud formations were supposed to have a cooling effect on the waters. Humboldt made temperature measurements, concluding that the water was cooler than the air and thus could not be cooled by it. He also observed that surface temperatures rose with increasing distance from the shore, concluding that the mass of cold water flowed from higher latitudes. This view was disputed by Bouganville in 1837; in 1844, de Tesson suggested an upwelling of the lower layers of water might account for the low surface temperatures.

The publication of observations by European visitors and naturalists in the New World reflects a bias in favor of foreign information over local knowledge. The first comprehensive report on the wonders of the New World was Fernandez de Oviedo's 1526 *Natural History of the West Indies*. Its great popularity in Europe stimulated the imagination of many future colonizers. Oviedo's work marked the beginning of a period of reports

that continued into the middle of the 19th century, by which time Linnaeus developed his system of binomial nomenclature, providing the mechanism for classification of living entities.

During the middle of the 19th century, the interest of maritime nations in exploring marine resource frontiers (mainly seals and whales), in charting the waters to reach and exploit the resources, and in studying the existence of life in the deep sea, led to several expeditions — the most important for Latin America being the U.S. Exploring Expedition (1838-42), Darwin's voyage aboard the *Beagle* (1831-36), the *Challenger* Expedition (1872-76), the work by Alexander Agassiz on board the *Blake* (1877-80), and the work of the *Albatross* over a number of years. The majority of this research fell in the area of marine biology, with physical, chemical, and geological aspects developing largely during the 20th century.

During the 19th century, virtually all the research that was being done in Latin American waters was conducted by foreign maritime powers; almost nothing was contributed by Latin countries. The abundance of land resources combined with relatively small populations meant there was little need for ocean exploration. To this day, agriculture based on inexpensive labor continues to be the most important aspect of Latin American economies, with political power generally concentrated among the landed aristocracy. Although several capitals and major cities have been founded along the coasts, an awareness of the potential of the oceans is only a very recent phenomenon. Fishing has always been relegated to the lower social and economic strata and disdained as a form of servile manual labor.

Spain controlled its immigration to the colonies so that it could maintain the purity of the ruling stock, preserve the wealth, and have a strong voice in church affairs. The historical circumstances that were adverse for the development of western science in Spanish America existed well into the 19th century. The settlement of the interior of southern South America increased the need for immigrant labor and as political conditions became more stable, European immigration rose rapidly in the latter half of the century. This had a significant influence on the cultural environment and brought changes in the educational system. The early advance of science in Argentina, southern Brazil, and Chile can be traced to European immigrants and their interest in developing the resources of their new homelands. It was in these countries where concern for the oceans developed around the turn of the century; Mexico, too, showed interest in developing its marine resources, benefiting from its close proximity to the United States.

While the foundations for marine biological investigations in the United States were laid at the end of the 19th century, Latin America's scientific



Pizarro  
(The Bettmann Archive, Inc.)

interests were limited mostly to botanical studies. Prior to World War I, basic work on the propagation of sound in the water was being investigated in several countries (see *Oceanus*, Vol. 20, No. 2, p. 8); Germany's development soon after of submarine warfare prompted the Allies to speed up their study of underwater sound as a method of detecting U-Boats. The war had a fundamental effect on three events. First, the flow of information from European universities and the training of scientists in Europe were reduced. This caused greater self-reliance in the United States. Second, there was a mobilization of scientific talent among the Allies to study all naval problems related to submarines. And third, the U.S. government firmly established the precedent of strong support for marine science.

As World War I began, Latin America was still completely dependent on European and, to a lesser extent, American technology and science. Only in the area of medicine was there significant Latin accomplishments. Not being directly involved in the war, Latin American governments found no pressing need to develop a naval science or technology. The educational system, classical in nature and relatively unaffected by European scientific pursuits, was scientifically stagnant. Furthermore, there was no need, indeed no desire,



to support the development of indigenous science. The children of the ruling minorities were generally educated abroad. National educational programs found only limited support. The system was geared toward preparing young aristocrats for traditional professions and commercial undertakings, which directly or indirectly perpetuated the oligarchies. A career in the sciences was an extremely rare choice.

The scientific progress that did take place in Latin America — and there was some — developed mainly because of the determination of a few persistent, outstanding individuals rather than from national commitments. The development of science in Latin America also suffered because of the isolation from new discoveries as well as from the neglect of the international scientific community.

### The 20th Century

The spread of western science in Latin America has occurred in three progressively overlapping stages — foreign exploration and investigation, the establishment of a dependent colonial science (founded on advances made abroad and adopted locally), and the completion of the process of transplantation. In the marine sciences, most Latin American countries are evolving from the first to the second stage, with Mexico, Argentina, and Chile moving into the third stage. The main emphasis in all countries is overwhelmingly in the area of marine biology, with concentration on taxonomic studies strongly influenced by specialists working in Europe and the United States. Other disciplines are still very weak in most countries, with the exception of Argentina, Brazil, Venezuela, Colombia, and Mexico. The Lamont-Doherty Geological Observatory at Columbia University in New York State and the Woods Hole Oceanographic Institution have aided these latter countries in the development of their marine science programs.

The emphasis on biological work can be traced to the influence of immigrants in southern South America, who promoted the study of local faunas and trained a generation of biologists. This is in marked contrast to the United States where scientific talents were mobilized to deal with the oceanographic demands of two world wars, which greatly expanded the fields of marine geology, physical and chemical oceanography, and meteorology.

The period of foreign coastal exploration and the charting of Latin American coastal regions was followed by the establishment of hydrographic offices at the turn of the 20th century; then, there was a period marked by preliminary observations and the establishment of natural history collections, after which came the biological institutes, most importantly the University of Chile's Montemar marine biological station at Viña del Mar in 1941, and, in 1946, the University of São Paulo's

Oceanographic Institute. The Institute of Marine Biology at Mar del Plata in Argentina was not established until 1960 (Table 1).

Latin America's fear of exploitation of its marine resources by foreign powers led to jurisdictional pronouncements. In 1952, Peru, Chile, and Ecuador issued the Declaration of Santiago, establishing 200-mile territorial waters. The concern over resources also resulted in the creation of the Permanent Commission for the South Pacific, which promoted the development of fisheries institutes, such as Ecuador's Instituto Nacional de Pesca (1961), Chile's Instituto de Fomento Pesquero (1963), and Peru's Instituto del Mar (1964).

The first Latin American congress on marine biology took place in Viña del Mar, Chile, in 1949. But the need for inter-American cooperation in the field was not recognized until a conference in Caracas, Venezuela, in 1954. A conference document recommended the creation of an Inter-American Oceanographic Institute (to be located in the Galápagos Islands) under the authority of a central Oceanographic Commission; additional regional centers would study biological, fishery, and ecological problems. At this time, only Argentina, Brazil, Chile, Cuba, Ecuador, Mexico, Peru, and Venezuela were actively interested in marine resources. The first meeting of general marine specialists took place in São Paulo, Brazil, in 1955. Under the auspices of the Panamerican Institute of Geography and History, a subsequent meeting of the working group on oceanography was held in Washington in March of that year. This meeting produced a report that emphasized the need for cooperation and exploration in the marine field and also identified areas of interest. In 1956, preliminary national reports on the resources of the continental shelf were presented at a conference in the Dominican Republic; the coordination responsibility for these activities was delegated to a representative oceanographic committee, headquartered in Mexico City, Mexico. Later that year, the first meeting of UNESCO's\* International Advisory Committee on Marine Sciences took place in Lima, Peru. The 1957 International Geophysical Year had the effect of strengthening scientific cooperation and, by this time, the United Nations was playing an important role in scientific efforts. In 1960, UNESCO's semiautonomous coordinating Intergovernmental Oceanographic Commission (IOC) was established to advise, promote, and catalyze ocean-related endeavors. Also, UNESCO's operational Division of Marine Science, upon request by member states, was charged with promoting research programs, disseminating information, and strengthening national

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\*United Nations Educational, Scientific, and Cultural Organization.

Table 1. Distinguished marine institutions in Latin America and date of founding.

<b>Argentina</b>		<b>Puerto Rico</b>	
Museo "Bernardino Rivadavia" Estación Hidrobiológica de Puerto Quequen	1923	Departamento de Ciencias Marinas, Universidad de Puerto Rico	1954
Instituto Antártico Argentino	1951		
Instituto de Biología Marina, Mar del Plata (INIDEP)	1960	<b>Venezuela</b>	
Centro de Investigación de Biología Marina	1961	Instituto Oceanográfico, Universidad de Oriente	1959
Comision Nacional de Estudios Geoheliofisicos Centro Nacional Patagónico	1968	Estacion de Investigaciones Marinas, Fundación La Salle	1960
Instituto Argentino de Oceanografía	1969		
<b>Brazil</b>		<p>infrastructures, with emphasis on education and training. These tasks were performed in cooperation with the United Nations Development Program. During the 1960s, the Latin American countries that had neglected their marine affairs in the past became actively involved. Joint research investigations were undertaken with oceanographic institutions, such as the Scripps Institution of Oceanography, Oregon State University, the Woods Hole Oceanographic Institution, Lamont-Doherty, and the University of Miami; major faunal surveys were conducted in tropical shelves and in deep-sea waters. Regional conferences, training courses, and seminars were held throughout South America. The period of the mid-1960s also was characterized by the creation of national oceanographic commissions in Latin America to coordinate national and international efforts. The Food and Agriculture Organization (FAO) of the United Nations was by this time playing a major advisory role in developing Latin America's fisheries. National fishery institutes were created, some undergraduate marine programs were initiated, and students began to go abroad for advanced training, mostly with support from international scholarships. In 1968, the need for international cooperation was addressed by efforts like the Cooperative Investigations for the Caribbean Sea and Adjacent Regions (CICAR). These efforts were not too cooperative nor investigative, but regional governments became more attuned to the concept of international marine research and more important, became more realistic about their own potential for harvesting and protecting marine resources, and their own scientific and technical limitations for addressing these efforts.</p> <p>In 1970, the United States launched the concept of the International Decade for Ocean Exploration (IDOE[see <i>Oceanus</i>, Vol. 23, No. 1]) which was approved by the United Nations to operate within the framework of a comprehensive long-term program of scientific investigation. Latin American countries became participants in several of the IDOE programs (Table 2). In addition, the Organization of American States (OAS) contributed funds for fellowships and for equipment needs</p>	
Instituto Oceanográfico, Universidade de São Paulo	1946		
Departamento de Oceanografía, U. Federal Pernambuco	1952		
Laboratorio de Ciencias do Mar, U. Federal Ceara	1960		
Instituto de Pesquisas da Marinha, Rio de Janeiro	1962		
Base Oceanográfica Atlântica, Rio Grande do Sul	1971		
<b>Chile</b>			
Estacion de Biología Marina, Montemar, Viña del Mar, Universidad de Chile	1941		
Departamento de Biología Marina y Oceanografía, Universidad de Concepción	1957		
Instituto de Fomento Pesquero	1963		
<b>Colombia</b>			
Instituto de Investigaciones Marinas, Punta de Betin	1966		
<b>Cuba</b>			
Centro de Investigaciones Pesqueras	1952		
Instituto de Oceanología	1959		
<b>Ecuador</b>			
Instituto Nacional de Pesca	1961		
Instituto Oceanográfico de la Armada	1972		
<b>Mexico</b>			
Instituto Nacional de Pesca	1962		
Centro de Ciencias del Mar y Limnología Universidad Nacional Autónoma de México	1973		
Centro de Investigación Científica y Educación Superior de Ensenada	1975		
Instituto Oceanográfico de la Armada	1978		
<b>Peru</b>			
Instituto del Mar del Peru	1964		



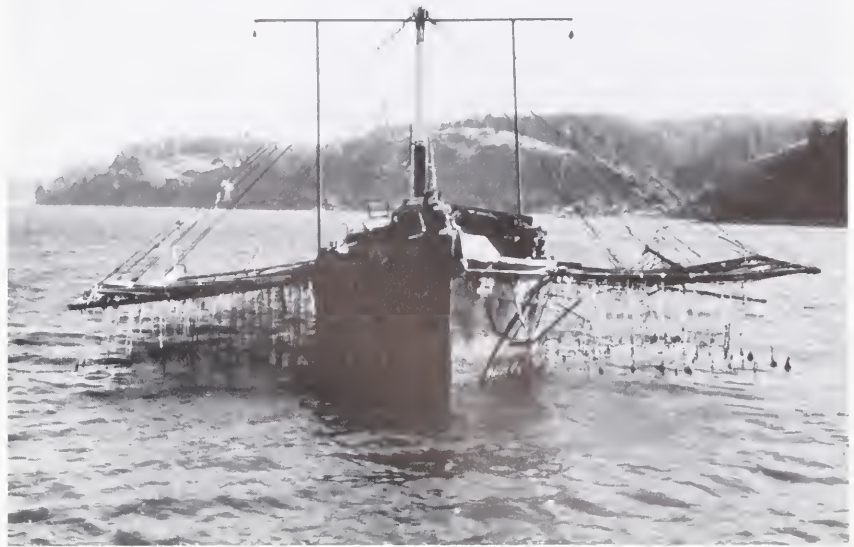
Table 2. International oceanographic participation by Latin American countries. (Source: UNESCO-IOC)

	International Decade for Ocean Exploration										LEPOR			
	IOC Membership	Environmental Forecasting		Environmental Quality		Seabed Assessment			Living Resources		Ocean Charting	Stock Assessment	Southern Ocean	IOCARIBE
		Subtropical Convergence	El Niño GARP-GATE	Baseline Studies	GIMPE	Continental Margins	Nazca Plate	Ocean Minerals	CUEA					
Argentina	x	x				x					x	x	x	
Bahamas														
Barbados														
Belize														
Bolivia (landlocked)			x				x				x		x	x
Brazil	x		x		x	x					x		x	x
Chile	x	x					x				x		x	
Colombia	x		x	x		x			x					x
Costa Rica	x													x
Cuba	x													x
Ecuador	x		x				x		x					
El Salvador														
France (Guadeloupe/Martinique)														x
Guatemala	x													x
Guyana														
Haiti	x													x
Honduras														
Jamaica	x					x								x
Mexico	x		x						x					x
Netherland Antilles	x													x
Nicaragua														
Panama	x						x							x
Peru	x		x	x										
Rep. Dominicana	x													x
Surinam														x
Trinidad & Tobago	x													x
Uruguay	x			x		x								
Venezuela	x					x	x	x	x					x

within its Multinational Marine Science Program. In the course of the IDOE, it was clear that most Latin American countries were insufficiently prepared to participate both scientifically and financially in oceanographic programs as understood within the IDOE. Moreover, the promise of initial United States funding, estimated at \$100 million to fully implement the program, was only fulfilled with \$15 million. Thus, although an effective machinery developed for multinational cooperation, the original hopes of a truly international scientific program fell short of expectations, and the growth of oceanographic competence in developing countries played a much smaller role than originally envisioned. Finally, in addition to the important efforts of the Organization of American States to promote cooperation and interchange, there have been development activities promoted by INTERCIENCIA, the federation of Associations for the Advancement of Science in the Americas (Brazil, Canada, Colombia, Costa Rica, Jamaica, Mexico,

the United States, and Venezuela), the Latin American Association for Biological Oceanography, and by the Latin American Committee for Marine and Aquatic Products of SELA, the Economic System for Latin America.

In brief, the Latin American countries have emphasized their need for marine science and technology and have looked to the International Oceanographic Committee to satisfy those needs, but the IOC does not have the mandate to adequately meet these demands. Moreover, the financial resources available under UNESCO's regular program are insufficient to meet these needs. Additional requests for assistance have been submitted to the Food and Agriculture Organization, the United Nations Development Program, and the UN Environmental Program (UNEP). The latter is particularly active in the area of environmental quality through its Regional Seas Program, and within its efforts with ECLA, the Economic Commission for Latin America. The UN



*Mussel culture experiment in Dichato, Chile.*

Office of Ocean Economics and Technology also has been active in promoting awareness of the problems of the coastal zones in Latin America.

#### **A Need to Look Inward**

The growth of marine science in Latin America over the last 30 years, mostly in the area of biology as we have stated, has been characterized by a weakness of national commitments, with high expectations and responsibilities being placed on the efforts of international bodies. No amount of funds or technical support from international organizations can produce effective benefits without a willingness on the part of national governments to utilize their own available means of developing their marine capability. Support for science, *per se*, has only developed in the last few years, and then only in a few countries. In fact, in view of the difficulties, the efforts and advances made by some marine institutions in Latin America have been remarkable. Government support has been mostly aimed at developing fisheries, with limited allocations for the scientific component needed to exploit them effectively.

The Peruvian experience is a case in point. Support for basic scientific development relative to the value of the fisheries was insignificant; ultimate responsibility fell on FAO specialists and international panels. Whereas the international missions were partly successful, mismanagement at the policy level contributed significantly to the collapse of the Peruvian fisheries. Furthermore, the export of two thirds of Latin America's fish harvest raises doubts about the sincerity of the concern for the region's protein deficiencies, lending credibility to claims that, at least in the countries with highest

catches, the hard currency gained by fishery exports are being used to finance military expenditures. There also is interest in developing aquaculture, but the emphasis has been on high-valued crustaceans for export. The true potential of food for the rural poor is not being fully explored.

One of the fundamental barriers to the growth of marine science in Latin America is the lack of national science policies that would create an appropriate environment for scientific development. Although some progress has been made, the key factor, and one difficult to assess, is quality. When one has to labor under adverse cultural circumstances, deficient basic scientific training, and a lack of science policies and government support, it is difficult to produce work of exceptional quality. The common result is the production of second-class science. This regrettable reality is the rule rather than the exception in the field of marine sciences in Latin America. The truth is that many of the region's marine institutions represent fragmented, disorganized scientific communities, poorly sustained, intellectually isolated, and generally directed toward irrelevant goals. Fortunately, the intellectual potential is quite promising; but the distribution of intellectual resources is independent of the political and economic factors needed to bring them to fruition. There are now some 50 Ph.D.-level marine scientists in Latin America, all working arduously to develop the field in their respective countries. Most are quite young; they have not yet reached the decisionmaking levels that would allow them to change and improve their environments. But there is reason for optimism: their impact should be felt within the next decade.





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#### Mañana

The pursuit of oceanographic investigations, as we have known them during this century, will probably come to an end with adoption of a United Nations-sponsored Law of the Sea treaty. Indeed, the way in which these expeditions and investigations are undertaken has already changed in the last few years. The new legal, organizational, administrative, and financial requirements that must be satisfied will probably impede, discourage, or foil future scientific oceanic ventures. Commercial undertakings, too, will probably only be conducted within strict international legal conditions. Consequently, three factors will affect marine research efforts in the coastal areas: the definition of economic zones, the growing impact of man's activities on coastal ecosystems and resources, and the high cost of the operation of vessels as a result of spiraling fuel prices. Thus, the outlook for Latin America is one in which there will be an emphasis on coastal living, mineral, and nonextractive resources.

The development of an infrastructure for the study, exploitation, and wise utilization of the coastal resources poses an interesting challenge for most Latin American countries. Those countries without, or with incipient, marine capabilities will have to adopt effective science policies to create the circumstances within which marine resources can be incorporated into the process of development. And those countries with some capabilities will have to strengthen or develop the appropriate mechanisms to exploit their growing expertise.

In addressing their common scientific problems (with a few distinguished exceptions),

Latin American governments and institutions must forgo the usual practice of "band aid" solutions (dependence on international specialists or nominal participation in grandiose, and often ineffective, international projects in the hope that somehow their people will be trained for them). Indeed, the most debilitating characteristic of most developing countries is not the per capita income, or their comparatively low gross national product, but their almost complete dependence upon external sources (imported science and technology) to solve their problems.

Thus Latin American countries must make a determined effort to develop their indigenous marine scientific competence, with critical attention to quality rather than quantity. During most international marine conferences, one hears with tedious repetition the dire need for trained scientists, technicians, and managers, as if these were obstacles that could not be overcome, or that should be mainly overcome by international organizations. There is not only a lack of national commitment to train people but there is also a failure to use them properly once they are trained. Indeed, there are many cases in which people that have received advanced training find it extremely difficult to do scientific work in their home countries. As a result, they often choose to accept slow, comfortable bureaucratization, or leave for other countries where their scientific pursuits can be fulfilled under less stifling conditions.

With a few exceptions, the university marine biological programs in Latin America are inadequate at the undergraduate level, usually requiring early specialization in fisheries, where, for example, cookbook population dynamics are taught. The fundamentals of scientific work are often neglected and the interdisciplinary nature of oceanography is



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disregarded. Indeed, the university is conceived of only as a transmitter of knowledge, whatever its value and time lag, and the university's organic function, the generation of new knowledge through scientific research, is overlooked. The university programs — whether called undergraduate, graduate, or professional — thus produce an oversupply of deficient graduates that are neither scientists nor marine or fisheries biologists. Graduates, often talented people disabled by their mediocre training, face several alternatives: a) they fill government research posts in fisheries departments or institutes; b) they often take better paying jobs in the fishing industry where little or no research is done; c) some remain as instructors, where they propagate a second-class education; d) others obtain support for advanced training, eventually returning to the same circumstances, but with most of the employment opportunities already filled; and e) a few end up in a field completely unrelated to their four or five years of education, representing a significant national waste.

The institutes themselves are usually the product of a politically motivated decision rather than of a science policy program. Adequate funds are initially approved to construct attractive buildings that are ceremoniously inaugurated. The facilities generally are poorly equipped (although in some cases they are overequipped — unused instruments being shown to visitors with hazy predictions as to their eventual use), and usually extremely deficient in library materials. During times of economic difficulties, support for scientific activities is not forthcoming; budgets are significantly reduced; in a few years, this produces a scientifically isolated and demoralized group of individuals, struggling with administrations to allow them to accomplish the duties for which they were hired. Under these conditions, the fine work that is occasionally produced is quite meritorious.

There are significant latent intellectual resources in Latin America that could be developed if the right circumstances were provided. Scientists would produce prodigiously if only given the appropriate framework and environment. If, in seeking to wisely manage their marine resources, Latin American countries do not drastically modify their approach to scientific education, institutional development, and the well-being of their scientists, the factors that are negatively affecting the development of science in general, and the marine sciences in particular, will be perpetuated. This is a most somber possibility. Oceanographic institutions, advanced academic centers, and international organizations can contribute to bring about the necessary changes, but the central decisions to alter the status quo must come from within the countries themselves.

The Organization of American States is



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currently planning a new program for marine science and resource development in Latin America. It has subdivided the region into four areas with, presumably, similar characteristics and problems. The areas are: Central America, the Caribbean island countries, Atlantic South America, and Pacific South America. The program focuses on the coastal zone. Table 3 summarizes some of the elements that are being considered. Six targets for action have been identified: ecosystems research and resource mapping; renewable and nonrenewable resources management; underutilized living and mineral resource development; socioeconomic analysis of resource development; recovery of degraded environments; and identification of alternative marine resource development possibilities. To work effectively, the OAS program must operate at government level, and of course, the implementation of any such program is subject to national capabilities.

Finally, because of the high priority given in Latin America to living marine resources, it is appropriate to briefly review this sector. Data collected by the Interamerican Development Bank (IDB) indicate that in 1978 fishery production amounted to 7.5 million tons, with an approximate landing value of \$2 billion. The IDB estimates that some 2 million people are engaged in fishing activities, the majority being coastal fisherman. The theoretical supply is 22 kilos per person, but the actual average human consumption is only 7 kilos — that is, two thirds of the region's production is being exported or processed for animal or industrial use. These estimates do not include post-harvest losses that result from lack of an infrastructure, estimated to reach as high as 30 percent in some countries, or that result from inappropriate technologies, for



example, by-catch losses of up to 70 percent by the shrimp industry. The IDB further estimates that if it is assumed that 25 percent of Latin America's protein deficiency (about 20 million gross tons of edible meats or 2 million tons of net animal protein per year) could be satisfied with relatively inexpensive fishery products, 5 million tons of fish would have to be produced. The region's potential, estimated by the FAO, is approximately 7 to 8 million tons per year, excluding krill. A 75 percent increase over current production would be needed, requiring an investment of about \$3 billion. If the present rate of human consumption were maintained through 1990, with an 8.5 kilos per capita demand, 2 million tons of additional fish should be caught — that is, a doubling of the present harvest for direct human use, and an added investment of about \$1.2 billion.

Considerable research will be needed to continue and expand exploitation of living resources. In the tropical countries, there has only been progress in the last decade toward identifying some of the mechanisms for the production of organic material; in higher latitudes, the recent discovery by Victor Gallardo of Chile of a filamentous sulfide bacteria that may play a previously unknown trophic role will probably require a reevaluation of the mechanisms of primary production. Throughout Latin America, man's often conflicting demands will undoubtedly require basic ecological information to provide alternatives for coastal zone management. In areas of large fishery harvests, the long-term fluctuations of fish populations must be understood so that the economic, social, technical, and industrial components of the fisheries can be efficiently

**Table 3. Summary assessment of elements of a marine resource development program for Latin America.**

Resource	Mineral	Living	Non-Extractive
Assessment Needs	Petroleum Natural gas Manganese nodules Sulphur Fresh water Construction materials Magnesium Other Bromine, iodine Phosphorite Barite Heavy metals	Human consumption Industrial Botanical Aquaculture Biochemical derivatives	Energy Recreation Transportation Communication Receptacle for waste
Implications	Inventories Extraction technology Geologists Engineers Support needs Industrialization	Ecosystem analysis Bioproductivity Stocks Dynamics Upwelling Technology Support Needs	Ocean waves/tides Thermal gradients Support activities Ports/harbors/marinas Industrial/urban/ agricultural discharges
Regional Diagnosis			
Caribbean Sea	Limited Trinidad-oil Bahamas-bauxite	Limited Insular species Diversification needs	Recreational high Thermal gradients
Central America	Unassessed Mexico more advanced	Underexploited Technological limitations	Recreational Waste receptacle
Atlantic S.A.	Potentially good Low exploration density	Important Underexploited	Energy, transportation Waste receptacle, critical focal areas
Pacific S.A.	Potentially good	Very important Diversification needs Industrialization	Energy/transportation Waste receptacle

managed. Substantial investments based on inadequate scientific understanding of the various populations and their interactions with the environment can lead to disastrous economic problems, examples of which are already in evidence.

Much remains to be learned. The only way in which Latin American nations can successfully incorporate the oceans into their development process is to make a determined commitment of substance rather than of form, generating the necessary knowledge from their own bank of human resources.

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#### Non-Resource Dimension

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Ecological interrelationships  
Economic impact  
Analysis of alternatives  
Social constraints and impact  
Legal aspects, national and international  
Institutional aspects  
Education and training  
Cultural characteristics  
Aesthetic considerations  
Coastal zone management information  
Conflicting uses and pollution

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#### Science policies

Education and technical training  
Integral planning and coordination  
Balanced development and economic planning  
Policy guidelines for resource utilization  
Research and institutional infrastructure  
Public education and awareness

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#### Scientifically very limited

Problems critical  
Weak economics

Incipient awareness of problems  
Serious pesticide problems in west coast  
Caribbean coast neglected

Improving capabilities, some institutional  
difficulties, poor coordination

Socio-political and management problems  
Institutional difficulties

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# Cilia and

by Sidney Tamm

Cilia and flagella are threadlike, usually microscopic projections of cells, specialized to perform whiplike or undulatory motions. Found throughout the animal kingdom, their beating serves to propel small organisms, such as a *paramecium*, through a liquid medium, or, when the ciliated cells are anchored in a tissue, to move fluids and particles over the surface of the epithelium. The human body uses cilia extensively for fluid transport in the respiratory and reproductive systems; many human sensory cells contain cilia or ciliary derivatives; and the human sperm swims by means of its flagellum. In many invertebrate animals, cilia and flagella perform an even wider variety of functions, including maintenance of water currents for feeding and gas exchange, transport of gametes, food and excretory products, various kinds of sensory reception, and locomotion. Like muscle contraction, the activity of cilia and flagella can be modified by the organism, resulting in adaptive responses to environmental stimuli.

The mechanism of ciliary and flagellar motion, and the means by which their activity is regulated, are therefore fundamental to our understanding of various life processes, as well as disturbances in these functions caused by disease or genetic defects (such as certain forms of human sterility). Cilia and flagella also are useful to study for a more general reason. Their motile machinery is made of an ordered array of microtubules. Microtubules are rigid, hollow cylindrical structures present in nearly all cells. They play an important role in determining cell shape and form, distributing the DNA of the chromosomes at cell division, and aiding or directing the transport of materials within cells and cell processes, such as nerve axons. Cilia and flagella provide a model system for investigating the role of microtubules in these fundamental forms of cell movement.

Ctenophores, or comb jellies, are among the most beautiful and voracious of the marine plankton. They consume enormous quantities of copepods, fish larvae, and other planktonic forms,



and thus are an important part of oceanic food chains. Ctenophores come in many shapes and sizes (Figure 1), but almost all propel themselves through the water by eight rows of ciliary paddles, called comb plates. Each comb plate, or cten, consists of a transverse band of thousands of long cilia, up to 2 millimeters in length, which beat together as a unit. Ctenophores are the largest known animals that use cilia for locomotion, and the longest cilia are found in the comb plates of ctenophores. Because the microscopic size of most other cilia makes them hard to study, the bigger cilia of ctenophores are indeed better, and comb plates are, according to G. A. Horridge, "one of those examples, occasionally presented in the animal kingdom, where a giant structure lends itself to the

Figure 1. Diversity of form and behavior in ctenophores. Small sea-gooseberries, or *Pleurobrachia*, upper left, catch copepods with their long tentacles; they are swallowed whole by large *Beroë*, upper right. The belt-like *Venus' girdle*, or *Cestum*, lower left, reaches a length of 1 meter, and can swim like an eel. *Leucothea*, a lobate ctenophore with oral lobes, lower right, has muscular fingers that dart out to paralyze passing plankton.

# Ctenophores



analysis of general biophysical problems." Both locomotory and sensory functions of cilia have been exploited in many of the behavioral responses of ctenophores, such as orientation to gravity, escape reactions, and feeding behavior. Ctenophores also are among the lowest animals with a nervous system, and several ciliary responses are under neural control.

Thus ctenophores provide many unique advantages for studying mechanisms of ciliary motion, sensory functions of cilia, and control and coordination of ciliary activity. Conversely, the study of cilia in ctenophores reveals much about the behavior and physiology of this important group of marine animals.

## Mechanism of Ciliary Coordination

Cilia beat with a rapid, straight-armed effective or power stroke, which moves the water, followed by a slower, curling recovery or return stroke (Figure 2). Adjacent cilia characteristically beat one after another in a regular sequence, resulting in metachronal (out-of-phase) waves of ciliary activity that sweep across the ciliated surface. Since at any one time some cilia are always performing a power stroke, metachronal coordination ensures a uniform and continuous propulsive force.

Ctenophores are the classic material for experimental investigations on the mechanism of ciliary coordination, because their ciliary units, or comb plates, are relatively large and widely spaced. The comb rows run from the sense organ at the aboral end of the body to the mouth at the opposite (oral) end (Figures 1 and 2). The comb plates beat in an orderly sequence, starting at the aboral ends of the rows and proceeding orally (Figures 2 and 8). Metachronal ciliary waves therefore travel down the comb rows in an aboral-oral direction. The effective stroke of the plates is normally in the opposite direction — toward the aboral pole. Consequently, the animal swims mouth foremost.

Two opposing theories of ciliary coordination have been proposed, based largely on experiments with ctenophores. In 1890, the German physiologist Max Verworn found that preventing the movement of comb plates in *Beroë*, a pink, dirigible-shaped ctenophore (Figure 1), stopped transmission of ciliary waves. Cutting across a comb row between two plates did not interrupt coordination, however. Verworn proposed that the plates are coordinated by mechanical interaction, — that is, the movement of one plate stimulates the next plate to beat by hydrodynamic drag forces transmitted through the seawater.

Working at the Marine Biological Laboratory in Woods Hole, Massachusetts, the Harvard physiologist G. H. Parker showed in 1906 that metachronal waves were propagated past immobilized plates of *Mnemiopsis*, a ctenophore possessing oral lobes (lobate). This led him to propose a neuroid or epithelial conduction mechanism, in which a nervelike impulse conducted through the tissue itself triggers the beating of successive plates. Subsequently, both mechanical and neuroid theories have been used to explain not only metachronism of comb plates, but also ciliary coordination in other systems.

This controversy has recently been resolved. More detailed microsurgical experiments on ctenophores by myself and others have provided direct evidence for the mechanical theory of coordination (Figure 3). In *Beroë* and *Pleurobrachia* (Figure 1) (but not in *Mnemiopsis* and other lobate



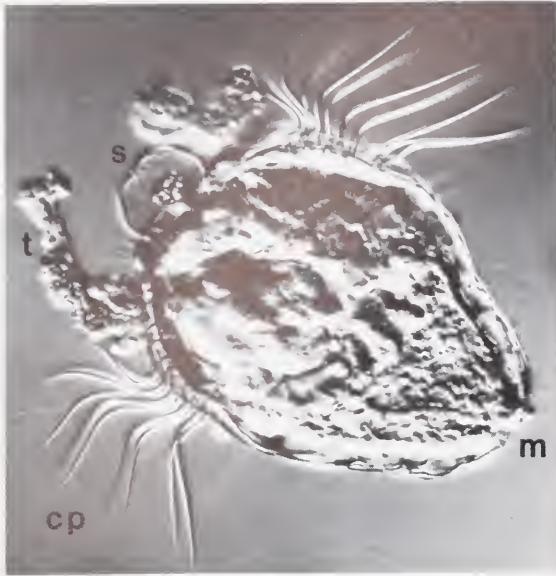


Figure 2. Forward-swimming cydippid larva of *Pleurobrachia*. Note the prominent statocyst (s) at the aboral pole, and mouth (m) at the oral end of the larva. Rows of ciliary comb plates (cp) are caught in profile by electronic flash. In this photograph, the plates nearest the aboral pole have already performed an effective stroke, and are unrolling toward the mouth in a recovery stroke. Plates closer to the oral end are "frozen" in late to middle stages of the effective stroke. The two tentacles (t) are partially retracted. Magnification 350x.

ctenophores), preventing the movement of comb plates, amputating plates near the base so that just the stubs beat, or increasing the distance between plates, stops transmission of metachronal waves; however, a narrow cut through the tissue between plates does not interrupt wave propagation (Figure 3, Table 1). The comb plates are mechanosensitive, and beat when touched. In fact, Michael Sleight of the University of Bristol in England was able to show that the beat frequency and the angular velocity of beating can be directly controlled by a mechanical stimulator vibrating at set frequencies.

Therefore, the comb plates of *Beroë* and *Pleurobrachia* are triggered to beat by hydrodynamic drag forces arising from the movements of the plates themselves. This group of ctenophores offers the best demonstration of mechanical ciliary coordination in any system and, as such, illustrates a fundamental property of the ciliary motor. Mechanical triggering or phasing of beating means that the motile machinery can be activated and timed by mechanical forces. Current explanations of bend propagation along cilia and flagella postulate that force generation is controlled locally by internal mechanical stress arising from curvature changes. By demonstrating a built-in mechanosensitivity of the motile machinery,

ctenophore comb plates provide strong evidence for such a sensory-motor feedback mechanism in cilia.

But what is the mechanism of ciliary coordination in lobate ctenophores? The same experiments on *Pleurobrachia* and *Beroë* give opposite results when done on lobates such as *Mnemiopsis*, *Bolinopsis*, and *Leucothea* (Figure 3 and Table 1). This is the reason for the earlier dispute: previous researchers had not recognized this dichotomy, and had attempted to interpret the experiments on all ctenophores by one and the same mechanism. Parker's view that mechanical interaction between the plates does not coordinate them in lobates has been confirmed (Table 1). The key to the problem lies in a narrow tract of short cilia, the interplate ciliated groove, which runs between successive plates in lobate ctenophores, but not in other types. Microsurgical experiments show that this ciliated pathway is responsible for coordinating the activity of the comb plates (Figure 3 and Table 1). The question then arises: how are the cilia of the groove coordinated? According to recent findings, they are coordinated mechanically. It is not yet clear how the ciliated groove stimulates beating of a plate, but this may also be done by mechanical interaction. If so, the neuroid or epithelial conduction theory would suffer a gelatinous death in the very animal that gave rise to it. This is not to say that epithelial conduction does not occur; George Mackie of the University of Victoria and others have demonstrated its importance in mediating various effector responses in other invertebrates and in vertebrate embryos. Epithelial conduction does not seem to coordinate the beating of cilia, however. In addition, recent electrophysiological studies have shown that electrical events do not coordinate ciliary activity in single-celled organisms, such as *Paramecium*.

One may then ask, why do lobate ctenophores use this second type of comb plate coordination? The reason seems to be that the interplate ciliated groove allows coordination between plates that have become widely separated as a result of damage to the comb rows. In the laboratory, we have found that removal of a piece of a comb row results in rapid closing of the wound, and a dramatic increase in the distance between comb plates next to the original excision (Figure 3j). In *Beroë*, *Pleurobrachia*, and other species lacking an interplate ciliated groove, coordination between plates is not restored until new plates regenerate in the gap, a process that takes more than a week. In lobates, however, coordination reappears as soon as the wound heals (one to two days), because the stretched ciliated groove conducts waves across the gap between the plates. Lobates are known to be more fragile than other ctenophores, and are commonly found with widely spaced plates, indicating previous damage to the rows. Because it

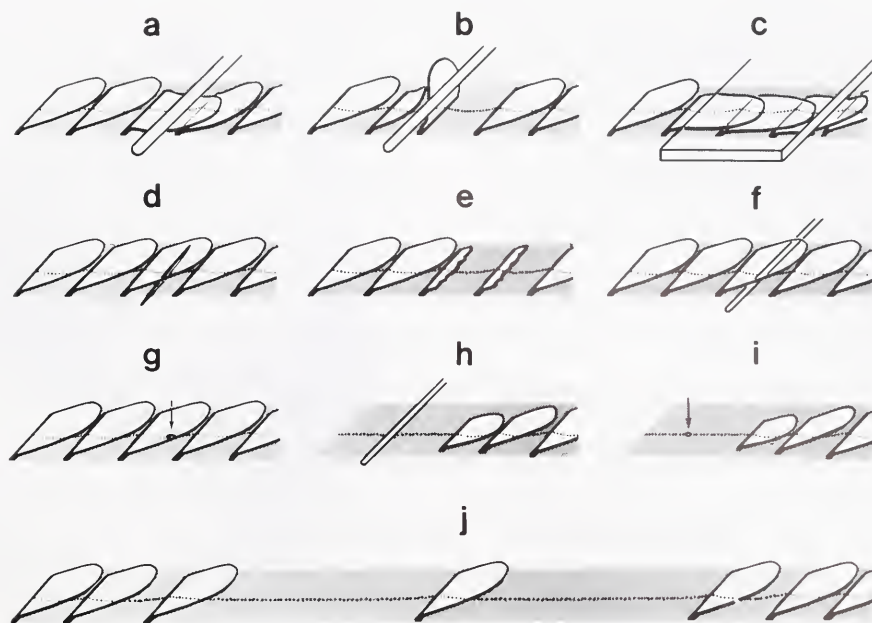


Figure 3. Microsurgical experiments to test the mechanism of ciliary coordination. Dotted line represents the interplate ciliated groove in the comb rows of lobates. (See Table 1) (From Tamm, 1973)

permits the rapid restoration of coordination across such gaps, the interplate ciliated groove is probably an adaptation to the more delicate gelatinous body of this group of ctenophores.

Interestingly, the free-swimming cydippid larvae of lobates resemble miniature *Pleurobrachia*, and likewise do not possess an interplate ciliated groove. Nevertheless, their comb plates are

coordinated. Thus the type of ciliary coordination changes during development in this group of ctenophores!

#### Mechanosensory Transduction by Motile Cilia

Like many other organisms, ctenophores can sense the direction of gravity and use it to modify their behavior. Ctenophores often assume a vertical

Table 1. Results of ciliary coordination experiments on ctenophores with and without an Interplate Ciliated Groove (ICG). (From Tamm, 1973)

Experiment	Shown in Figure 3	With ICG (Lobata)	Without ICG (Pleurobrachia, Beroë)
Prevent movement of comb plate(s) by:			
Pressing down one plate	a	+(-)*	-
Holding one plate upright	b	+	-
Pressing down several plates	c	+	-
Cut tissue between comb plates	d	-	+
Amputate comb plates	e	+	-
Increase the distance between plates	j	+	-
Prevent movement of ICG cilia	f	-	-
Cut the ICG	g	-	-
Prevent movement of ciliated groove cilia	h	-	-
Cut the ciliated groove	i	-	-

+ Transmission of metachronal waves

- Interruption of metachronal waves

\* When movement of the ICG cilia is also prevented



position with their aboral-oral axis parallel to the direction of gravity. During calm weather they are found at the surface in a resting or feeding position. When disturbed, ctenophores swim away from the surface, and in a container remain at the bottom, mouth facing downward. If a ctenophore is tilted from either position of vertical balance, it rights itself by asymmetrical frequencies of beating on uppermost and lowermost pairs of comb rows. If the animal turns to swim up, the lowermost rows beat faster than the uppermost ones; the converse occurs during downward steering. The tendency to swim up or down — that is, the sign of geotaxis — is called a mood.

Gravity receptors, or statocysts, generally consist of a movable mass, the statolith, in contact with ciliated receptor cells. Mechanical stimulation of the cilia by the weight of the statolith causes membrane conductance changes in the receptor cell. These generator or receptor potentials are transmitted by sensory nerves, and lead to appropriate behavioral responses. How mechanical stimuli are transduced into electrical signals is a major unsolved problem in sensory biology. Furthermore, because the cilia of some mechanoreceptors are actively motile, whereas those of others are not, the role that ciliary motility plays in mechanosensory transduction also is unknown.

The ctenophore statocyst has several unique advantages for our investigation of the mechanoreceptor function of motile cilia. The statocyst is located at the surface of the aboral pole, and is readily accessible for observation and experimental manipulations (Figures 2 and 4). The cilia themselves are arranged into four conspicuous groups, called balancers, which are more than 50 micrometers long and support a round statolith (Figure 4). The balancers are motile, and act as pacemakers for the comb rows. When a balancer beats, a single wave of beating is propagated by mechanical interaction along the two ciliated grooves connected to its base, and thence to the pair of comb rows in that quadrant of the body.

At the turn of the century, several researchers realized that geotaxis must somehow depend upon the motile responses of the balancers to deformation by the statolith. Recently these responses have been directly observed, and their effects on beat frequency of the comb rows quantitated in my laboratory at the Marine Biological Laboratory. By using a new device, the cteno-tilter, we have been able to precisely vary the orientation of the animal with respect to gravity (Figure 5). Films of the beat frequency of comb rows versus tilt angle of the ctenophore demonstrate that the geotactic response is caused by inhibitory and excitatory effects on beat frequency. For example, rotating a negatively geotactic animal from 180 degrees (all rows inactive) to a horizontal position

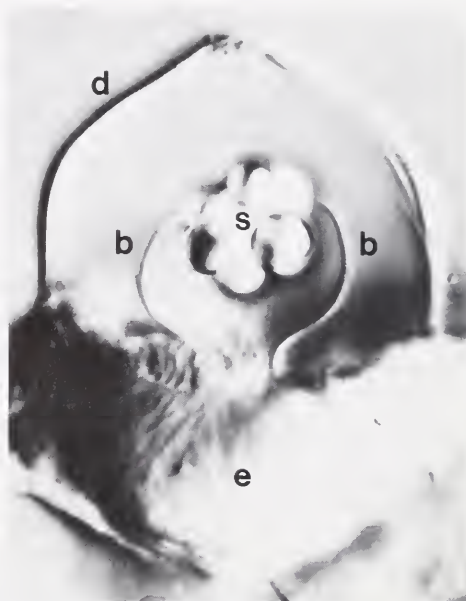


Figure 4. Statocyst of a *Pleurobrachia* larva. Two of the four sickle-shaped balancers (*b*) that support the cellular statolith (*s*) are visible. In adult statocysts, each balancer consists of a group of 150 to 200 cilia. A transparent dome of nonmotile cilia (*d*) encloses the statocyst, and prevents the escape of newly released statolith cells from the epithelial floor (*e*). Magnification 1,300x.

excites activity of the lowermost rows; tilting from 0 degrees (all rows active) to a horizontal position *inhibits* the beating of the uppermost rows (Figure 5, right). The same changes in orientation have the opposite effects in positively geotactic animals (Figure 5, left). Whether a given position will excite or inhibit beating thus depends on the mood. The ctenophore statocyst is primarily a static receptor, not an acceleration detector, since the frequency responses at a given position do not change with time.

The mechanical and motile responses of the balancers themselves have been visualized in cydippid larvae of ctenophores, which have a prominent statocyst and are particularly suitable for high-resolution microscopy (Figures 2 and 4). By using a micro-cydippid-tilter (Figure 6), we observed that the weight of the statolith deforms the distal part of the balancers, and increases or decreases their rate of beating, depending on the direction of deformation and the mood. In a negatively geotactic animal, for example, when a balancer is pulled away from the center of the statocyst, its beat frequency increases; when it is pulled toward the center, its rate of beating decreases.

Mechanosensitivity of the balancers may also be demonstrated by artificial mechanical stimuli. Bending a balancer with a fine tungsten needle

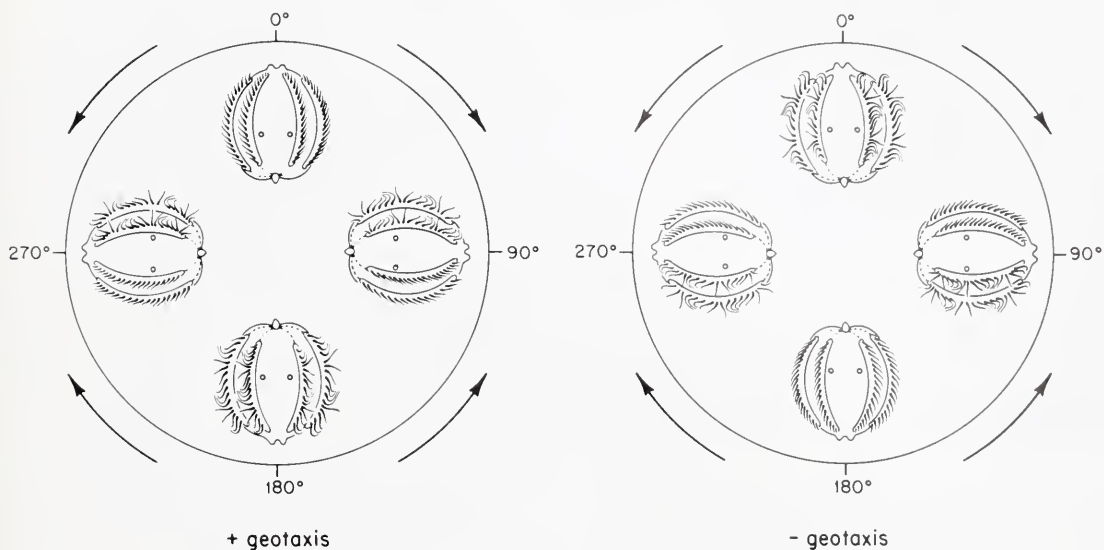


Figure 5. Geotactic responses of *Pleurobrachia*, as shown with the cteno-tilter. The ctenophore is pinned to a transparent disk that can be rotated in a vertical plane underwater. Relative beat frequencies of the comb rows, indicated by number of waves, during positive and negative geotaxis are shown for the two vertical and horizontal positions.

operated by a micromanipulator increases or decreases its beat frequency, depending on the direction of deformation and the mood. This change in frequency is transmitted to the appropriate pair of comb rows, thus mimicking a geotactic response.

Directional sensitivity is also typical of mechanotransduction in vertebrate hair cells, such as found in the lateral-line organs, vestibular organs, and auditory organs. Instead of a motile response, however, bending the hair bundle in one direction causes a depolarizing receptor potential, whereas displacement in the opposite direction results in a hyperpolarizing response. In addition, all other known mechanoreceptors do not reverse the sign of their directional sensitivity.

In hair cells and other statocysts that give electrical signals as their primary response, the receptor potentials are graded with amplitude of the displacement stimulus. In the ctenophore statocyst, where only motile responses are functionally expressed, one may ask: is the beat frequency of a balancer graded with the extent of its deformation? The cteno-tilter shows that it is (Figure 7). Both increases and decreases in the beat frequency of comb rows are approximately linear functions of tilt angle up to 40 to 50 degrees deviation from vertical. Thereafter, the maximum frequency response is maintained to the horizontal position.

As previously mentioned, the ability to reverse the sign of geotaxis is a unique feature of ctenophore mechanoreceptors. What is the mechanism of mood? Reversal in the frequency

response of a balancer to the same mechanical stimulus points to a change in the receptor (balancer) cell itself. In this regard, electrical stimulation of the whole statocyst causes rapid beating of all balancers and comb rows. This indicates that membrane conductance changes of the balancer cells can control the motility of the balancers. In addition, it has been known for a long time that changes in mood can be caused by a variety of stimuli, such as water turbulence, light intensity, and hydrostatic pressure.

Taken together, these findings suggest that reversal in directional sensitivity of the balancers is caused by electrical changes in the balancer cells, mediated by input from the nervous system. The effects of anesthetics, which block nervous responses, provide support for this view: without a functional nervous system, all animals become positively geotactic and do not change moods! Finally, electron microscopy reveals nerves in the statocyst that make numerous synaptic contacts onto the balancer cells.

Geotaxis in ctenophores thus appears to involve a novel combination of mechanosensory transduction and motility: a mechanoelectrical process, similar to that in other known mechanoreceptors; and an electrical-motile step, perhaps analogous to the recently discovered relationship between beat frequency and membrane potential in *Paramecium*. Nervous stimulation of the balancer cells, via input from various sensory receptors, apparently acts at the second step to cause reversals in the sign of geotaxis.



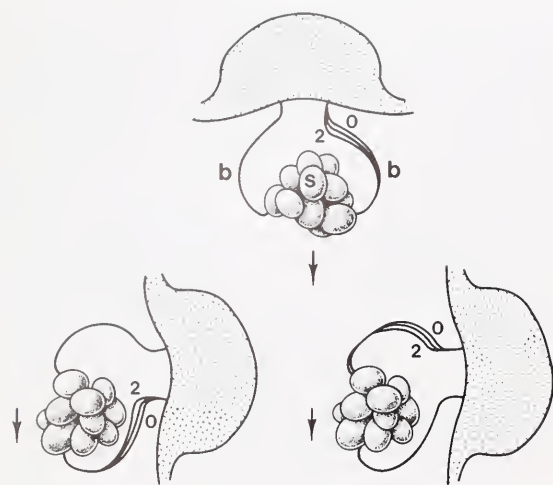


Figure 6. Deformations and motile responses of balancers (b) induced by the gravitational load of the statolith (s). A micro-cydidipid-tilter was made by placing a microscope slide of immobilized *Pleurobrachia* larvae on a vertical rotating stage of a horizontally oriented microscope. The responses were filmed at 200 frames per second to slow down the movements. Tracings 0-2 show the effective stroke of balancers at 5 millisecond intervals: 0 indicates resting position, 2 represents the maximum excursion. Top, ctenophore oriented in 0 degrees position (see also Figure 5). All four balancers beat at 9 hertz. Bottom left and right, positive geotactic response at 90 degrees. The lower balancer beats at 1 to 2 hertz (left); the upper balancer beats at 13 hertz (right).

### Control of Ciliary Beat Direction

Besides the regulation of beat frequency, as manifested by the geotactic response, other parameters of ciliary and flagellar activity can be controlled by the organism. These modifications in the beat pattern are transient responses to various environmental stimuli, and result in adaptive changes in behavior. Examples include changes in shape and symmetry of flagellar bending waves, during chemotactic turning of sperm; the ciliary arrest response which interrupts water flow and particle transport in filter feeders, such as mussels and ascidians; and changes in the direction of ciliary effective stroke, as in the avoiding reaction of *Paramecium* and ctenophores (Figure 8).

These diverse motor responses share a common basis: all are mediated by a transient increase in intracellular calcium concentration. However, the means by which calcium modifies the pattern of ciliary and flagellar motility is not understood, nor are the specific ciliary structures involved in the responses identified.

The problem of regulating ciliary and flagellar activity is closely related to the question of how they beat. A cilium or flagellum consists of a cylinder of nine doublet microtubules surrounding a central

pair of single microtubules, the entire 9 + 2 structure being held together by radial and circumferential linkages (Figure 9). A series of paired projections, called arms, are attached along one side of each outer doublet microtubule. The arms consist of the enzyme dynein, which can split adenosine triphosphate (ATP), the energy source for ciliary and flagellar movement.

From the work of Ian and Barbara Gibbons of the University of Hawaii's Kewalo Marine Laboratory, and Peter Satir of the Albert Einstein College of Medicine in the Bronx, New York, it is clear that the force for ciliary motion is generated by the relative sliding of doublet microtubules past one another, driven by the ATP-powered dynein arms which act as cyclic cross-bridges. Other structures linking the peripheral doublets to the central pair are thought to confine or restrain this local sliding, thereby converting translational movement into bending movement. Since all nine pairs of dynein arms are arranged uniformly around the periphery (Figure 9), and generate force in only one direction, arms on opposite sides of the cilium will act antagonistically with respect to bending. Most investigators therefore believe that bending in a given direction is caused by activation of the dynein arms on only one side of the cilium, whereas bending in the opposite direction is caused by active sliding of doublet microtubules on the other side.

How does this switching mechanism in cilia work? That is, how does calcium selectively activate sliding between different sets of doublet microtubules around the cilium? An attractive theory, based on studies showing a correlation between orientation of the central pair and direction of beating in protozoan cilia, is that calcium causes a rotation of the central pair, which acts as a distributor to signal sliding of doublet microtubules in sequence.

A critical test of this theory has been carried out recently with ctenophores. We discovered that stimuli which increase the flow of calcium into cells cause a 180-degree reversal in beat direction of the comb plates of cydidipid larvae (Figure 8). The larvae swim backwards for a short time, as in an avoiding reaction of *Paramecium*! Although ciliary reversal is common in protozoa, this is the first direct demonstration of it in multicellular animals.

Ctenophores have distinct advantages for analyzing the structural basis of beat direction. The comb plate cilia have unique morphological markers, not present in protozoan cilia, for identifying sidedness of the central pair and specific doublet microtubules (Figure 9). In addition, a single comb plate contains thousands of long cilia which beat synchronously, thereby facilitating transmission electron microscopy.

To do this work, we "froze" ciliary activity on forward and backward swimming larvae by a rapid

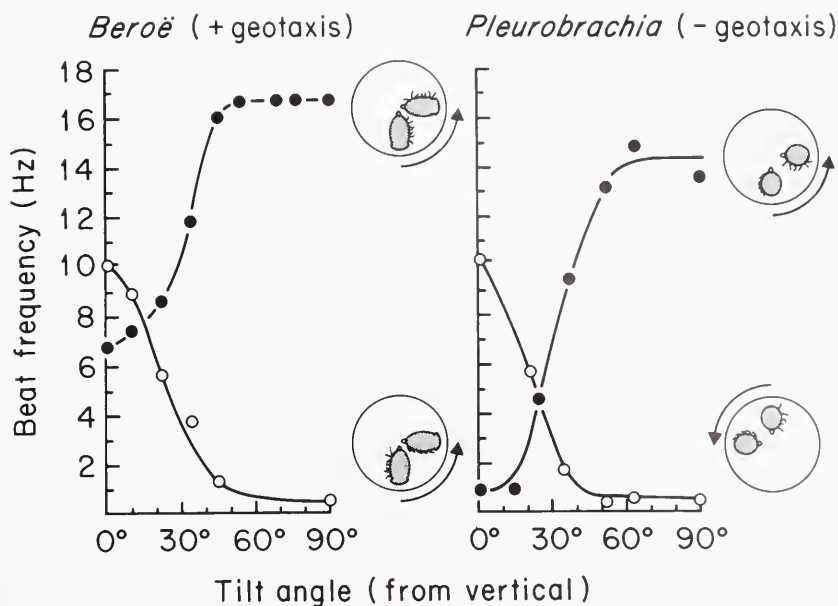


Figure 7. Quantitative analysis of geotactic responses using the ctenu-tilter. Beat frequency and tilt angle were determined from films.

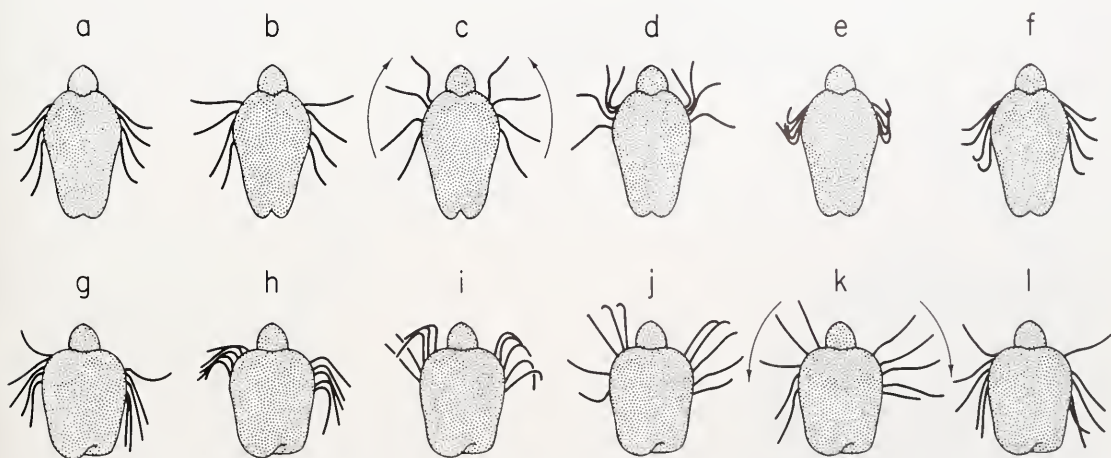


Figure 8. *Pleurobrachia* larvae swimming forward in seawater (top row, drawn at 60 millisecond intervals from film at 200 frames per second), and backward in seawater containing a high concentration of potassium chloride (bottom row, drawn at 8 millisecond intervals from film at 400 frames per second). During forward swimming (a-f), the effective stroke of the comb plates is directed aborally (arrows in c), and the plates unroll toward the mouth in the recovery stroke. During backward swimming (g-l), the beat is reversed 180 degrees toward the mouth (arrows in j, k). Successive plates are triggered to beat in an aboral-oral sequence during normal swimming, top row, and in the reverse order during backward locomotion, bottom row.





Figure 9. Transverse section through comb plate cilia of ctenophore larvae. In addition to the 9 + 2 arrangement of microtubules (shown in cross-section), comb plate cilia have compartmenting lamellae (cl) that connect doublet microtubules No. 3 and No. 8 of adjacent cilia into rows running normal to the plane of bending. Also, a dense midfilament (mf) is located on only one side of the central pair. During forward swimming, the effective stroke (ES) is directed aborally, toward doublets Nos. 5 and 6 and away from the midfilament. During backward locomotion, the effective stroke is directed orally, toward doublet No. 1 and the midfilament. Thus neither the central pair nor the peripheral doublets rotate when beat direction reverses.

chemical fixation technique. The orientation of the ciliary markers with respect to the direction of beating was determined by electron microscopy of transverse thin sections through the comb plates. If the orientation of the central pair really controls the direction of bending, then during a 180-degree ciliary reversal, it should also rotate 180 degrees. We found, however, that reversal of beat direction is

not accompanied by 180-degree rotation of the central pair or of the nine doublet microtubules (Figure 9).

This clear-cut result shows that the orientation of the central pair does not control the direction of ciliary bending — that is, which doublets actively slide and which do not.  $\text{Ca}^{++}$  may therefore act directly on the sliding process itself by differentially activating dynein ATPase activity around the cilium. Although the central pair may still determine the plane of bending, it now seems likely that its orientation is only a passive consequence of the bending.

We also discovered a second type of ciliary reversal response specific to the feeding behavior of adult *Pleurobrachia* (Figure 10). When a *Pleurobrachia* catches prey (such as copepods) with one of its long tentacles, the tentacle immediately contracts. The two comb rows on either side of the food-carrying tentacle then beat in the reversed direction at high frequency, sweeping it toward the mouth. The other six comb rows continue to beat in the normal direction; as a result, the ctenophore spins toward the food-capturing tentacle, further wrapping the prey into the mouth. Reversed beating only lasts a short time, after which the animal resumes forward swimming.

Thus when copepods are fed to pinned *Pleurobrachia*, which are unable to rotate, the unilateral ciliary reversal response can be analyzed by high-speed cinemicrography, microsurgery, and electrophysiology. Together with the anatomical studies by Mari-Luz Hernandez-Nicaise of the Université Claude Bernard, Villeurbanne, France,

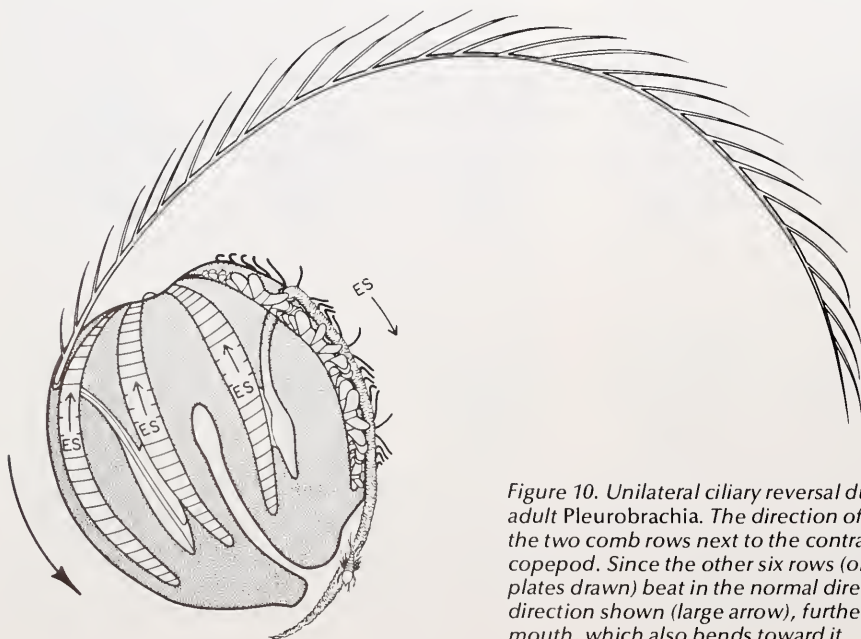


Figure 10. Unilateral ciliary reversal during the feeding response of adult *Pleurobrachia*. The direction of effective stroke (ES) reverses in the two comb rows next to the contracted tentacle that bears the copepod. Since the other six rows (only three shown here without plates drawn) beat in the normal direction, the animal spins in the direction shown (large arrow), further wrapping the prey into the mouth, which also bends toward it.

the results so far indicate that unilateral ciliary reversal is mediated by a local nervous pathway that leads from either tentacle to the two adjacent subtentacular comb rows.

Although inhibitory and excitatory responses of cilia have been shown to be under nervous control in various animals, including ctenophores, this would be the first clear example of ciliary reversal controlled by nerves (whether or not the nervous system plays a role in triggering the global ciliary reversal response in ctenophore larvae is not yet known).

Thus ctenophores have told us a great deal about how cilia work. We also have seen some of the marvelous behaviors that cilia can bestow upon these animals. In the words of Dr. Sebastian Beroë of the Stazione Zoologica in Naples, "cilia and ctenophores, like love and marriage, go together like a horse and carriage."

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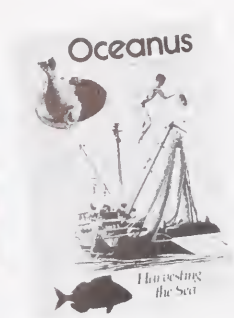
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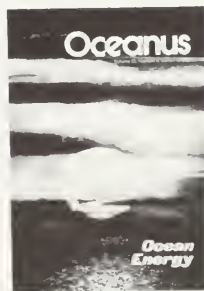
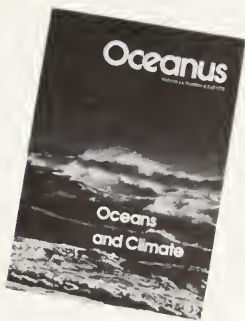
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